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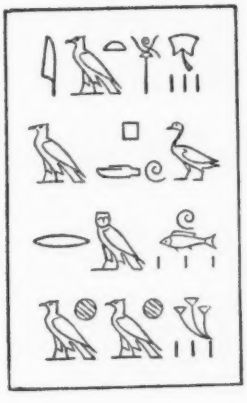

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THE JOURNAL OF WILDLIFE MANAGEMENT

VOLUME 22 OCTOBER 1958 NUMBER 4

DISTRIBUTION OF POPULATIONS AND HUNTING KILL OF THE CANVASBACK

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INTRODUCTION

In order to understand the basic requirements for survival and maintenance of waterfowl populations, it is essential to determine their distribution on the breeding and wintering grounds, and to define the more important migration routes and harvest areas of the various population segments. This information, along with the knowledge of mortality and productivity, is necessary for management of the canvasback (*Aythya valisineria*) as a resource for hunting and other recreational uses. Such management practices as the creation of refuges, habitat improvement, and the formulation of hunting regulations require an understanding of these factors.

Aerial surveys of breeding grounds and wintering areas, band recoveries, and a mail survey of waterfowl hunters were the primary source material in this study. References from the literature and personal communications also aided in delineating the breeding range.

The reliability of the results depends on the accuracy of the banding and survey data and on the validity of the assumptions made in their analysis. Most of the data originally were gathered for purposes requiring less accuracy than is desired here, and some are of unknown reliability. Since these procedures have not been described previously, nor the assumptions made in using them discussed, they are treated in this paper in considerable detail. The specific procedures followed are described in the main body of the paper. In order to maintain the continuity of the text, descriptions of the surveys, limitations of the data, and the assumptions made in their use are discussed in an appendix.

Information on populations and migration came from the co-operative effort of many government agencies, private organizations and individuals. Breeding-population indexes in Canada and Alaska were computed from aerial-survey data gathered by the Bureau of Sport Fisheries and Wildlife. Several aerial observers from the Canadian Wildlife Service and provincial governments assisted in the aerial surveys. Breeding-ground surveys in the United States were conducted by state personnel. Surveys of wintering populations (January inventories) were made through the co-operation of the Bureau of Sport Fisheries and Wildlife, Canadian Wildlife Service, and the various states. The accumulation of banding records resulted from efforts of Federal, state, and provincial agencies of the United States and Canada, plus private groups and individual co-operators. Canvasback recoveries include all records filed at the Bird Banding Office of the Bureau of Sport Fisheries and Wildlife through 1956 and certain recoveries during the 1957-58 hunting season. From most areas, these were from birds banded since 1945. The major exception was Louisiana, where all recoveries were from birds banded during 1930–41.

In describing the breeding and wintering ranges and migration routes, frequent reference is made to the physiographic regions described for the United States by Fenneman (1931, 1938), and for Canada by Putnam, *et al.* (1952). The various types

of prairie associations and the related aspen parklands referred to in the description of the major portion of the breeding range are those defined by Carpenter (1940).

Without the banding done by more than a hundred individuals associated with the agencies and groups listed above, this report could not have been written. Don P. Fankhauser assisted in organizing some of the band-recovery data. We also are indebted to other Bureau personnel for their helpful advice.

BREEDING RANGE OF THE CANVASBACK

Data from several sources were used in mapping the range of breeding canvasbacks. The boundaries of the range were derived from breeding records in the literature. Relative densities of birds within various units of the range were derived from the population data of the 1955 breeding-ground survey. The breeding-population index was computed for each 18-mile segment by adding: the number of birds in pairs; the number of single males or females, doubled; and the number of birds in flocks of mixed sexes. These records were plotted on a map and lines were drawn where breaks occurred between areas of apparently different population densities. The various regions of the breeding range that were delineated are shown in Fig. 1. Relative population densities of the regions then were derived from the average densities of birds in the transect segments. There were certain regions, such as the Dakotas, British Columbia, and portions of Alaska, for which survey data comparable to that for other regions were not available. For these regions, data from the literature and other surveys and the knowledge of persons familiar with the country were used in mapping estimated population densities. In plotting densities from breeding-ground-survey data, we assumed that the number of canvasbacks seen on each 18-mile segment of transect was a valid measure of the relative density of birds in the vicinity. No corrections were made for unidentified or unseen ducks. Since this method did not yield precise quantitative data, the densities of birds in the various regions were expressed by descriptive words rather than by numbers.

The major part of the range of breeding canvasbacks (Fig. 1) is in the northern Interior Plains of North America. It extends southeasterly from the mouth of the Mackenzie River through the boreal forest and prairie regions of west-central Canada into the prairies of the glaciated Missouri plateau and western lake section of the United States, and reaches a terminus in northwestern Iowa. In Canada, this large area of breeding range is bordered on the east by the Canadian Shield (Laurentian Upland) and on the west by the Rocky Mountains. Disjunct populations occur in the Rocky Mountains of Alaska, Yukon, and British Columbia; in the Rocky Mountains and northern portions of the intermontane region of the western United States; and in the Sand Hills of Nebraska.

Within the breeding range, canvasbacks are restricted largely to the various types of deep-water marsh that are characteristic of regions with a cool, subhumid climate. These marshes ordinarily are composed of fairly dense patches of coarse, emergent aquatic plants associated with adjacent areas of open water. Typical plant species include the hardstem bulrush (*Scirpus acutus*), broadleaf cattail (*Typha latifolia*), and reed (*Phragmites communis*).

The great majority of canvasbacks breed in the aspen parklands (prairie–forest ecotone) of Alberta, Saskatchewan, and Manitoba, and in the mixed-grass and tall-grass prairies of Saskatchewan, Manitoba, and northern North Dakota. Within this region, highest densities in 1955 were found in the pothole area in the vicinity of Minnedosa, Manitoba. Other breeding areas, in order of diminishing density were: other areas in the aspen parklands, mixed-grass prairies, and tall-grass prairies. High population densities were found in small, detached sections of other regions, including the Yukon Flats and Minto Lake areas of Alaska, the Old Crow Flats of Yukon, the Hay Lakes and Lake Claire–Athabaska delta areas of northern Alberta, and the Saskatchewan River

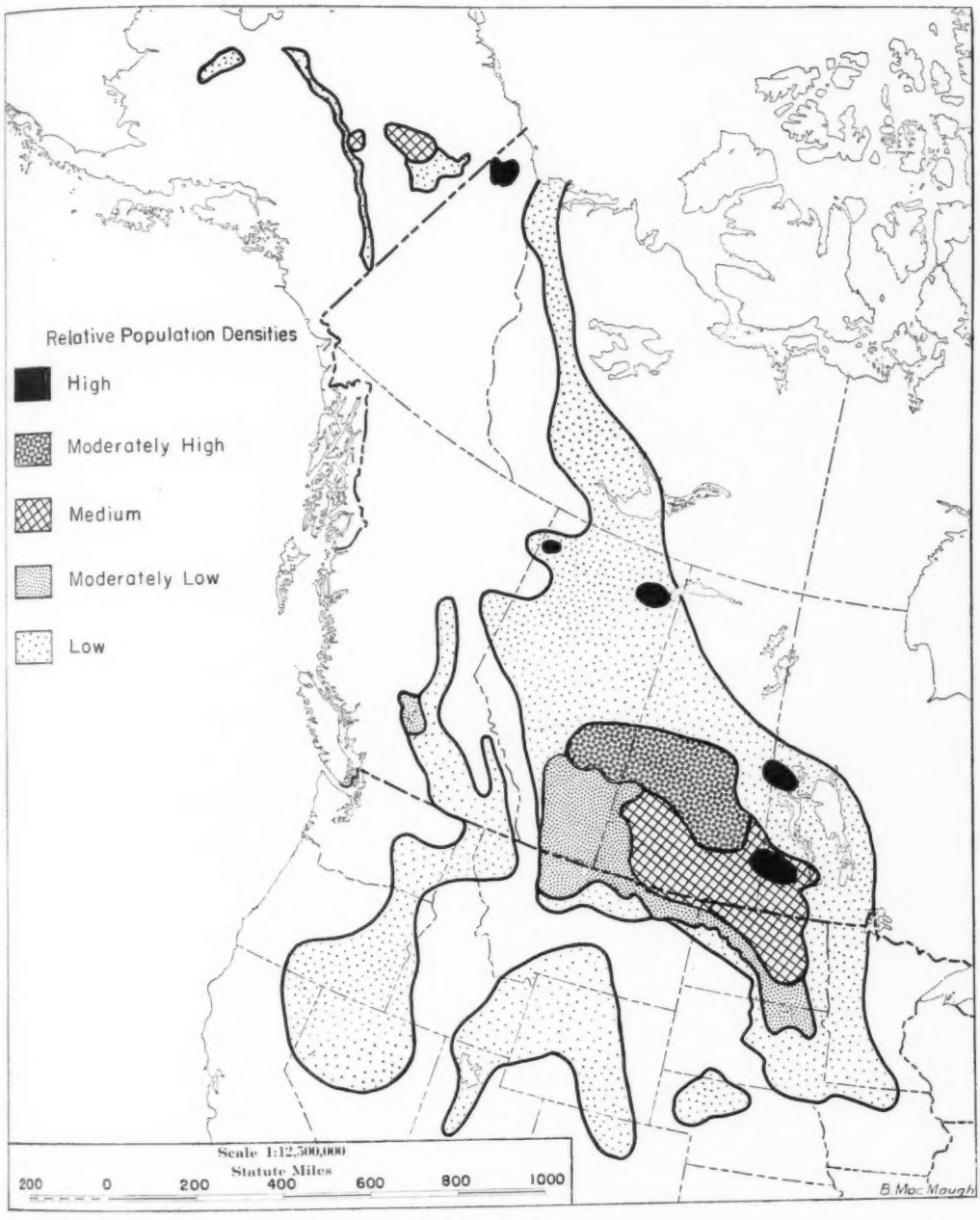

FIG. 1. Breeding range of the canvasback.

delta area on the Manitoba–Saskatchewan border. Moderate numbers also were found in the short-grass prairies of Alberta, Saskatchewan, and northern Montana; in the mixed-grass prairies of southern North Dakota and northern South Dakota; and in the Cariboo Parklands of British Columbia. Elsewhere within the range, the populations were quite low, localized, and often sporadic.

In order to obtain more definite numerical data concerning the number of canvasbacks,

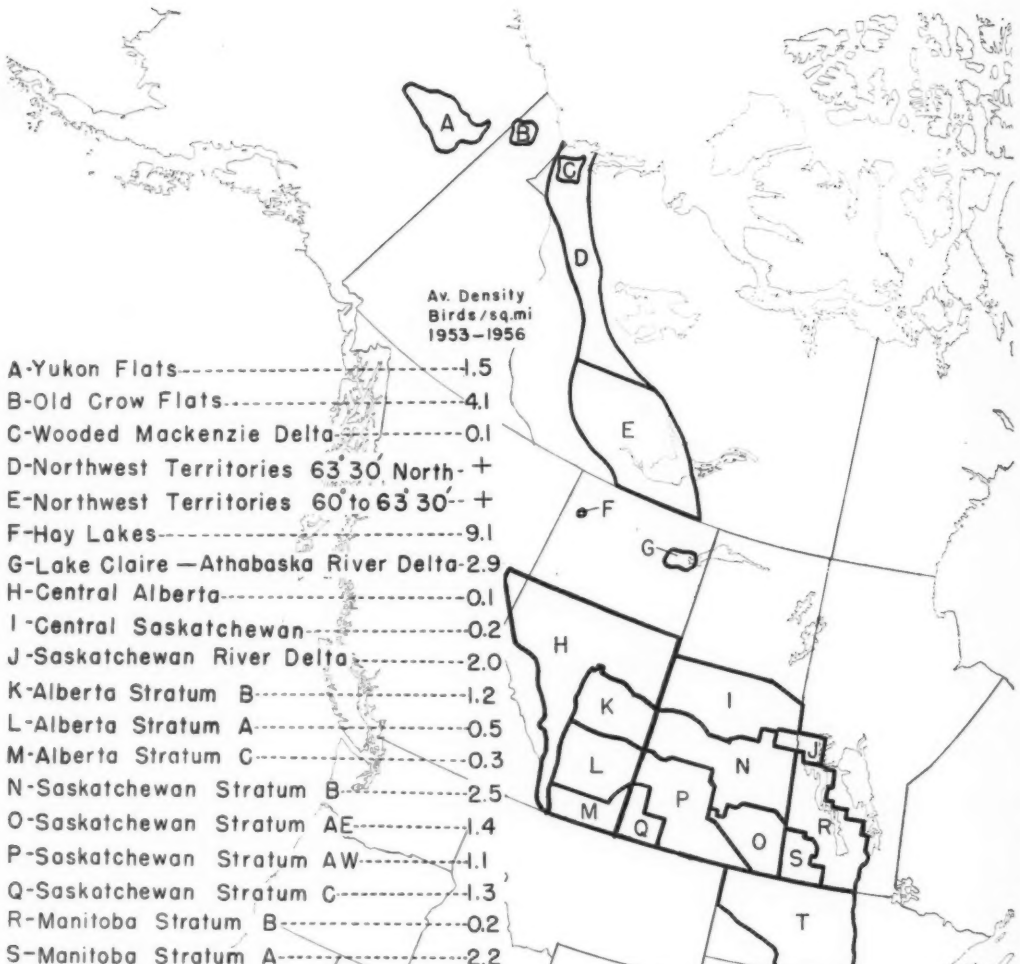

FIG. 2. Breeding population survey strata.

the records from the breeding-ground surveys were analyzed a second way. This second analysis made use of the population indexes that are obtained for each of the areas included in the surveys. These areas are referred to as strata. Their locations and names are shown in Fig. 2. The indexes are counts of birds in the areas, obtained by the methods described in the appendix. The indexes for the various strata in the years 1953–56 and the average number of birds per square mile are shown in Table 1. These index values give more precise numerical information on differences in the numbers of birds in different parts of the breeding range than was possible by the first method of analysis. They also permit comparison of numbers from year to year. They are

considered to be more reliable because they include data for four years rather than for one and also because corrections were made for unidentified ducks. On the other hand, the second method is less satisfactory than the first in that the populations in the strata are less homogeneous than those in the natural areas shown in Fig. 1. Despite these differences in the methods, conclusions from the two agree fairly well.

The population indexes in the various strata indicate that about three-fifths of the total breeding population of canvasbacks occurs in the aspen parklands of Alberta, Saskatchewan, and Manitoba. About one-fifth is found in the mixed-grass and tall-grass prairies of Saskatchewan and North Dakota. From a study of Table 1, it is apparent that the number of breeding canvasbacks varies from year to year, not only within individual strata but also in the whole survey area. We believe that the total index values for all strata combined, shown at the bottom of the columns in Table 1, are the most reliable indexes of canvasback numbers that are available at present. They show that the number of breeding canvasbacks remained fairly stable during the years 1953–56. The greatest deviation from the average occurred in 1954, when the index value was 13 per cent below average. The indexes for the individual strata were more variable than the total index. However, the indexes for strata representing the parkland areas (stratum B in Manitoba, Saskatchewan, and Alberta, stratum A in Manitoba, and stratum AE in Saskatchewan), which contain about three-

TABLE 1.—CANVASBACK BREEDING-POPULATION INDEXES

Strata	Averages 1953–56	Yearly Totals[1] 1953	1954	1955	1956	Areas (Sq. Miles)	Densities (Birds/ Sq. Mile)
Alaska-Yukon area							
Yukon Flats	8,900	2,800	14,700	6,600	11,600	5,800	1.5
Old Crow Flats	8,100	1,200	3,400	18,700	9,200	1,970	4.1
Northwest Territories							
Wooded Mackenzie Delta	500	1,000	1,000	0	0	3,600	0.1
63°30′ north to Mackenzie Delta	800	1,750	1,550	0	0	32,000[2]	+[3]
60° to 63°30′	1,600	1,700	2,200	2,200	0	35,000[2]	+
North-central Alberta							
Hay Lakes	2,200	2,500	2,000	—	—	200	9.1
Lake Claire–Athabaska Delta	5,800	5,100	6,900	7,600	4,000	2,000	2.9
Central Alberta	7,600	—	—	—	7,600	77,000	0.1
Central Saskatchewan	6,500	7,600	7,800	10,500	0	40,000[2]	0.2
Saskatchewan River Delta	7,900	9,900	5,300	11,000	5,400	3,960	2.0
Southern Alberta							
Stratum A	10,900	7,200	18,600	9,600	8,100	22,090	0.5
Stratum B	31,700	24,900	30,200	35,200	36,300	26,100	1.2
Stratum C	4,300	2,700	2,800	2,800	8,900	16,112	0.3
Southern Saskatchewan							
Stratum AW	42,400	62,100	20,800	31,700	55,100	37,630	1.1
Stratum AE	21,100	8,300	17,700	24,300	33,900	14,600	1.4
Stratum B	127,200	153,400	118,700	121,000	115,700	50,500	2.5
Stratum C	14,800	29,400	9,400	1,800	18,600	11,290	1.3
Southern Manitoba							
Stratum A	22,500	9,700	26,700	22,500	31,000	10,370	2.2
Stratum B	5,100	2,000	4,100	5,900	8,200	28,600	0.2
North Dakota	29,200	31,300	15,700	38,400	31,400	34,000	0.8
South Dakota	2,900	4,000	2,500	2,300	3,000	25,600	0.1
Nebraska Sand Hills	1,100	—	1,100	500	1,700	10,870	0.1
Totals	363,100	368,550	313,150	352,600	389,700	489,292	0.7

[1]Blank spaces indicate that no data were available. [2] Indicates only the area of that part of the strata occupied by canvasbacks. [3] Less than 0.05

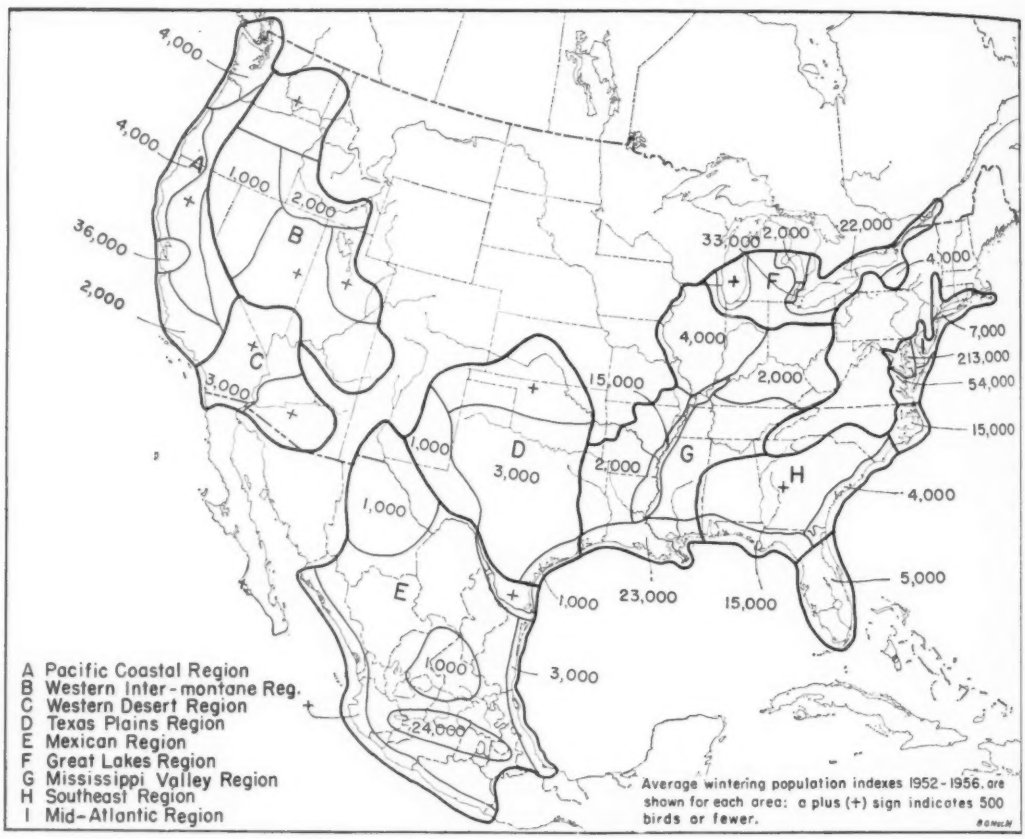

FIG. 3. Wintering range of the canvasback.

fifths of the entire breeding population, were much less variable than the indexes for the strata of the various grassland types or the Far North. We believe that the greater variability in the indexes for the secondary areas may have been produced in part by greater errors in sampling, and bias in the survey data for these areas.

WINTERING RANGE OF THE CANVASBACK

Wintering populations of canvasbacks occur over a wide area. They are found chiefly on the bays and estuaries of the Atlantic, Pacific, and Gulf coasts of the United States and Mexico. Canvasbacks winter also on the larger rivers, lakes, and reservoirs of the southern Great Lakes area, the lower Mississippi Valley, the southern plains, the western intermontane and desert areas, and central Mexico. These range data were obtained from the winter surveys that are described in the appendix. In order to facilitate the description of wintering populations, the entire winter range was divided into nine major regions (Fig. 3). These, listed in the order of their average estimated populations for the period 1952–56, are: Mid-Atlantic, Great Lakes, Mississippi Valley, Pacific coastal, Mexican, southeastern, Texas plains, western intermontane, and western desert regions. Each region was further subdivided into the sections outlined in Fig. 3, where the average estimated populations are shown also. Annual and average population estimates for each section are listed in Table 2. Individual birds found outside this range may be considered to be of casual or accidental occurrence.

From the winter surveys it was estimated that the average continental wintering population during the period 1952–56 was approximately 508,000 (Table 2). When the

estimates were analyzed by regions, it was found that about 83 per cent of the wintering canvasbacks occurred in the eastern third of the United States (including adjacent areas in southeastern Ontario), and only 17 per cent in the western United States and Mexico. The proportion of the total population found in each region was: Mid-Atlantic—57 per cent; Great Lakes—12; Mississippi Valley—9; Pacific coastal—9; Mexican—6; southeastern—5; Texas plains—1; western intermontane and western desert—1. The outstanding concentration areas were in the Chesapeake Bay sections. More than half of the average continental population of canvasbacks wintered here (42 per cent in the upper Chesapeake section and 11 per cent in the lower Chesapeake section). Other important concentration areas included the San Francisco Bay section (7 per cent), the southeastern Michigan section (6 per cent), the Mexican central plateau section (5 per cent), and the Mississippi Valley coastal section (5 per cent).

The total estimated size of wintering populations of canvasbacks varies from year to year, as is shown by the winter-survey figures for the period 1952–56 (Table 2). The minimum count of 384,000 reported for 1952, is 24 per cent below the mean of 508,000, while the maximum count of 669,000, reported for 1954, is 32 per cent above the mean. The yearly variation in regional populations is much more pronounced. Maximum and minimum population counts for the different regions in the different years varied respectively from their means as follows: Mid-Atlantic, 36 and 38 per cent; Great Lakes, 56 and 53; Mississippi Valley, 58 and 83; Pacific coastal, 40 and 38; Mexican, 44 and 62; southeastern, 42 and 33; Texas plains, 80 and 60; western intermontane and western desert, 67 and 100. It appears that estimated wintering populations of the Mid-Atlantic, Pacific coastal, and southeastern regions are comparatively stable, while those of the Mississippi Valley region, the arid Texas plains, western intermontane, and western desert regions fluctuate more widely.

Wintering populations of birds probably shift their ranges considerably from time to time. This is indicated by the inverse relationship between yearly population changes of the Mississippi Valley region and the Great Lakes region (Table 2). Similarly, unusually low counts in the Mid-Atlantic region in 1952, correlated with abnormally high counts in the Mississippi Valley region in the same year, suggest that major shifts in population sometimes take place between these regions. Local shifts in population apparently are fairly common, for increases often were recorded in certain sections of a region at the same time that declines were noted in other sections of the same region.

Reliability of the estimates of wintering populations unfortunately is unknown. Population fluctuations and shifts suggested by changes in the population estimates are therefore of unknown significance. The winter survey and its limitations are discussed in the appendix.

MIGRATORY MOVEMENTS OF BREEDING POPULATIONS

Information concerning migratory movements of canvasbacks was derived from an analysis of distant recoveries of birds that were banded at numerous banding stations throughout the breeding grounds. Distant recoveries were those of birds recaptured or killed outside the section of the breeding grounds where they were banded. To emphasize an important aspect of the biology of the canvasback, and for convenience in describing the various migratory patterns, the breeding range was divided into five major regions. The boundaries of most of these regions were defined by the locations of banding stations, the banded birds from which showed similar patterns of recovery distribution. Certain boundaries were based on very few banding stations. The boundaries of the north-central breeding grounds were arbitrarily located to encompass all banding stations contributing recoveries outside the area.

The general migratory movements from major regions are shown in Figs. 4–8. For this purpose each recovery from the region

TABLE 2.—WINTERING-POPULATION INDEXES OF CANVASBACKS (DATA FROM JANUARY INVENTORIES)[1]

Region and Section	Averages 1952–56	Yearly Totals				
		1952	1953	1954	1955	1956
Mid-Atlantic Region	*289,000*	*185,000*	*335,000*	*437,000*	*284,000*	*203,000*
N. Embayed	7,000	(6,000)	9,000	(7,000)	(9,000)	6,000
Upper Ches.	213,000	78,000	251,000	336,000	227,000	173,000
Lower Ches.	54,000	80,000	60,000	84,000	33,000	11,000
N.C. Embayed	15,000	21,000	15,000	10,000	15,000	13,000
Southeastern Region	*24,000*	*25,000*	*32,000*	*15,000*	*14,000*	*32,000*
Atlantic Sea-I.	4,000	(7,000)	(3,000)	4,000	(2,000)	3,000
Floridian	5,000	10,000	6,000	2,000	1,000	5,000
Gulf Coast	15,000	7,000	23,000	9,000	10,000	24,000
Interior	+	(1,000)	(+)	+	(1,000)	+
Miss. Valley Region	*48,000*	*88,000*	*30,000*	*65,000*	*23,000*	*33,000*
Coastal	23,000	51,000	20,000	28,000	(6,000)	10,000
Miss. River	15,000	(31,000)	3,000	23,000	(3,000)	17,000
Western Valley	2,000	(5,000)	1,000	1,000	(+)	2,000
Tenn. River	2,000	1,000	1,000	4,000	(+)	2,000
Ohio River	2,000	+	1,000	4,000	4,000	+
Upper Valley	4,000	+	4,000	5,000	10,000	2,000
Great Lakes Region	*62,000*	*27,000*	*90,000*	*59,000*	*95,000*	*37,000*
Eastern Great Lakes	22,000	(14,000)	34,000	(21,000)	(28,000)	15,000
N.Y. Finger Lakes	4,000	(3,000)	1,000	(6,000)	3,000	8,000
S.E. Michigan	33,000	0	54,000	32,000	63,000	14,000
Lake Huron	2,000	10,000	1,000	0	+	0
Lake Michigan	+	+	+	+	1,000	+
Texas Plains Region	*5,000*	*4,000*	*8,000*	*4,000*	*1,000*	*6,000*
Coastal	1,000	1,000	4,000	1,000	+	+
Lower Plains	3,000	1,000	3,000	3,000	1,000	5,000
Upper Plains	+	0	+	+	+	+
Pecos Valley	1,000	2,000	1,000	+	+	1,000

(Continued on next page)

is considered to be representative of the region as a whole, regardless of the exact location of the banding station from which it was derived. Each map shows the outline of the region and all distant recoveries of birds banded within it. Recoveries of canvasbacks that were banded in summer are separated into two categories, direct and indirect. Direct recoveries are those of birds recovered during the fall and winter immediately following the summer when they were banded, while indirect recoveries are those of birds recovered at any later time. The season of banding and season of recovery are shown on the maps. The seasons are defined as follows: summer—May 21 to August 20; fall—August 21 to December 20; winter—December 21 to February 20; spring—February 21 to May 20. These periods are based on information from the literature concerning breeding and wintering seasons and migration dates. None of the maps shows any appreciable difference in the distribution of direct and indirect recoveries. Although most of the banding records pertain to migratory movements during the fall, there were a few spring recoveries, and these suggest that the routes taken by spring and fall migrants are nearly identical.

Eastern breeding grounds (Fig. 4).—This portion of the breeding range extends from the Saskatchewan River delta through southern Manitoba, eastern North Dakota, western Minnesota, and northeastern South Dakota. Of the canvasbacks banded in this area in summer, 173 were recovered elsewhere. These included 126 banded in Mani-

TABLE 2.—WINTERING-POPULATION INDEXES OF CANVASBACKS (CONT'D.)

Region and Section	Averages 1952–56	Yearly Totals				
		1952	1953	1954	1955	1956
Mexican Region	*29,000*	*24,000*	*19,000*	*34,000*	*20,000*	*47,000*
Lower Río Grande	+	1,000	0	+	+	1,000
Upper Río Grande	1,000	4,000	+	+	1,000	+
Tableland	1,000	0	+	1,000	1,000	1,000
Central Plateau	24,000	10,000	17,000	31,000	17,000	43,000
Gulf Coast	3,000	9,000	2,000	2,000	1,000	2,000
Pacific Coast	+	+	0	+	+	+
Western Intermontane Region	*3,000*	*3,000*	+	*6,000*	*5,000*	*2,000*
Southern	+	0	+	0	0	+
Salt Lake	+	+	+	1,000	+	+
Western Great Basin	1,000	+	+	2,000	2,000	1,000
Snake River	2,000	2,000	+	3,000	3,000	1,000
Palouse	+	1,000	+	+	+	+
Western Desert Region	*3,000*	+	*2,000*	*6,000*	*3,000*	*3,000*
Southern California	3,000	+	2,000	6,000	3,000	2,000
Sonoran Desert	+	+	+	+	+	+
Mohave Desert	+	+	+	+	+	1,000
Pacific Coastal Region	*47,000*	*28,000*	*47,000*	*43,000*	*65,000*	*52,000*
Santa Barbara	2,000	+	2,000	6,000	2,000	1,000
San Francisco Bay	36,000	22,000	35,000	27,000	56,000	41,000
Redwood Coastal	4,000	3,000	3,000	4,000	4,000	8,000
Puget Sound	4,000	3,000	6,000	5,000	3,000	2,000
Interior	+	+	1,000	1,000	+	+
Totals	*508,000*	*384,000*	*563,000*	*669,000*	*510,000*	*415,000*

[1] Figures are rounded to the nearest 1,000. Numbers 500 or less are indicated by plus (+) signs. Figures in parentheses are derived in part from estimates of certain populations that were incompletely surveyed. The units within each region are outlined in Fig. 3.

toba, 11 in Saskatchewan, 15 in North Dakota, 18 in Minnesota, and 3 in South Dakota. In addition, 46 canvasbacks banded in fall and 2 banded in spring were recovered outside of the area. About four-fifths of the recoveries of birds banded in summer were made on the eastern wintering grounds (primarily the Great Lakes, Mid-Atlantic, and Mississippi Valley wintering areas) or along the migration routes leading to them. Most breeding canvasbacks from the eastern breeding grounds apparently migrate through Minnesota, Wisconsin, and the eastern Great Lakes and winter in the Chesapeake Bay area. This is indicated by the fact that the greatest concentrations of recoveries were reported from the Lake Winnebago area of Wisconsin (9 per cent), the Lake St. Clair–Detroit River area (14 per cent), and the upper Chesapeake section (26 per cent). Secondary flights occurred along the Mississippi Valley to the Louisiana coast, and through the Great Plains to Texas. The pattern of distribution of recoveries of canvasbacks banded in fall and spring was similar to that of birds banded in summer except that the numbers recorded along the Mississippi Valley and Great Plains routes were slightly higher. This suggests that many of these birds were banded as migrants and had originated in areas to the north or west of the eastern breeding grounds.

Central breeding grounds (Fig. 5).—This important area extends from eastern Alberta through southern Saskatchewan, northeastern Montana, northwestern and central North Dakota, and north-central South Dakota. There were 122 distant recoveries of canvasbacks banded in this area in summer. These included 1 banded in Alberta, 33 in southern Saskatchewan west of longi-

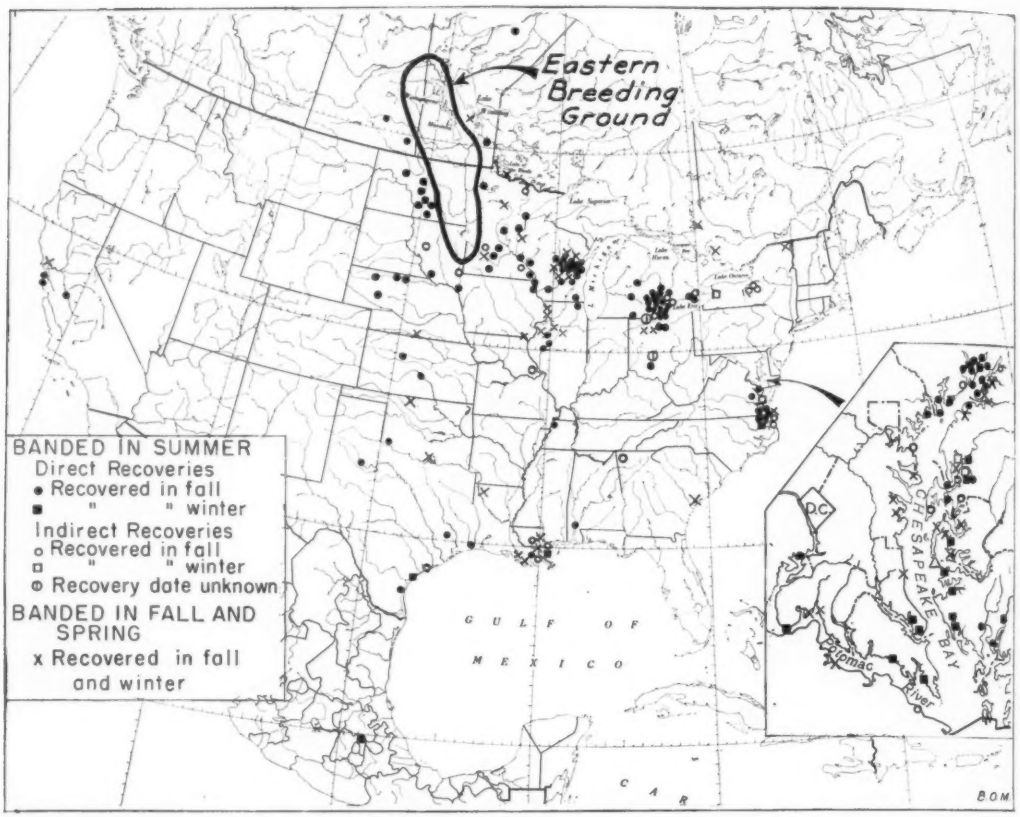

FIG. 4. Distribution of distant recoveries of canvasbacks banded on the eastern breeding grounds.

tude 105°, 55 in southern Saskatchewan east of longitude 105°, 2 in Montana, 24 in North Dakota, and 7 in South Dakota. In addition, 23 canvasbacks banded in fall and 6 banded in spring were recovered outside of the area.

About two-thirds of the recoveries of summer-banded canvasbacks were reported from the eastern wintering grounds (primarily the Great Lakes, Mid-Atlantic and Mississippi Valley regions) or along the migration routes leading to them. About one-fifth were reported from the central plains and from the wintering areas of Texas and Mexico; the remainder came from other areas to the west. Although the recoveries were widely scattered, the pattern of their distribution indicates that the majority of the canvasbacks from the central breeding grounds migrate in a southeasterly direction to the eastern Great Lakes and Chesapeake Bay wintering areas. Fairly large numbers migrate through the Great Plains to Texas and Mexico. Smaller numbers also travel to the lower Mississippi Valley and to San Francisco Bay. The distribution of recoveries of canvasbacks banded in fall and spring is similar to that of the birds banded in summer.

Western breeding grounds (Fig. 6).—This area includes most of the short-grass prairies and aspen parklands of southern Alberta, and the Cariboo Parklands of British Columbia. Of the canvasbacks banded in this area in summer, 45 were recovered elsewhere; 36 of these were banded in British Columbia and 9 in Alberta. In addition, 7 canvasbacks banded in the fall were recovered outside of the area. The majority of these birds migrate in a southwesterly direction, as indicated by the fact that four-fifths of the recoveries of summer-banded birds were made on or near the

Pacific Coast. Smaller numbers move to the Mid-Atlantic coastal area and the Texas plains. The greatest concentration of recoveries was reported from the San Francisco Bay area, which therefore probably is the principal wintering ground for this western segment of the canvasback population.

North-central breeding grounds (Fig. 7). —The Lake Claire–Athabaska delta area and portions of the boreal forest in eastern Alberta and west-central Saskatchewan are included in the north-central breeding grounds. Of the canvasbacks banded in this area in summer, 21 were recovered elsewhere, including 14 that were banded in

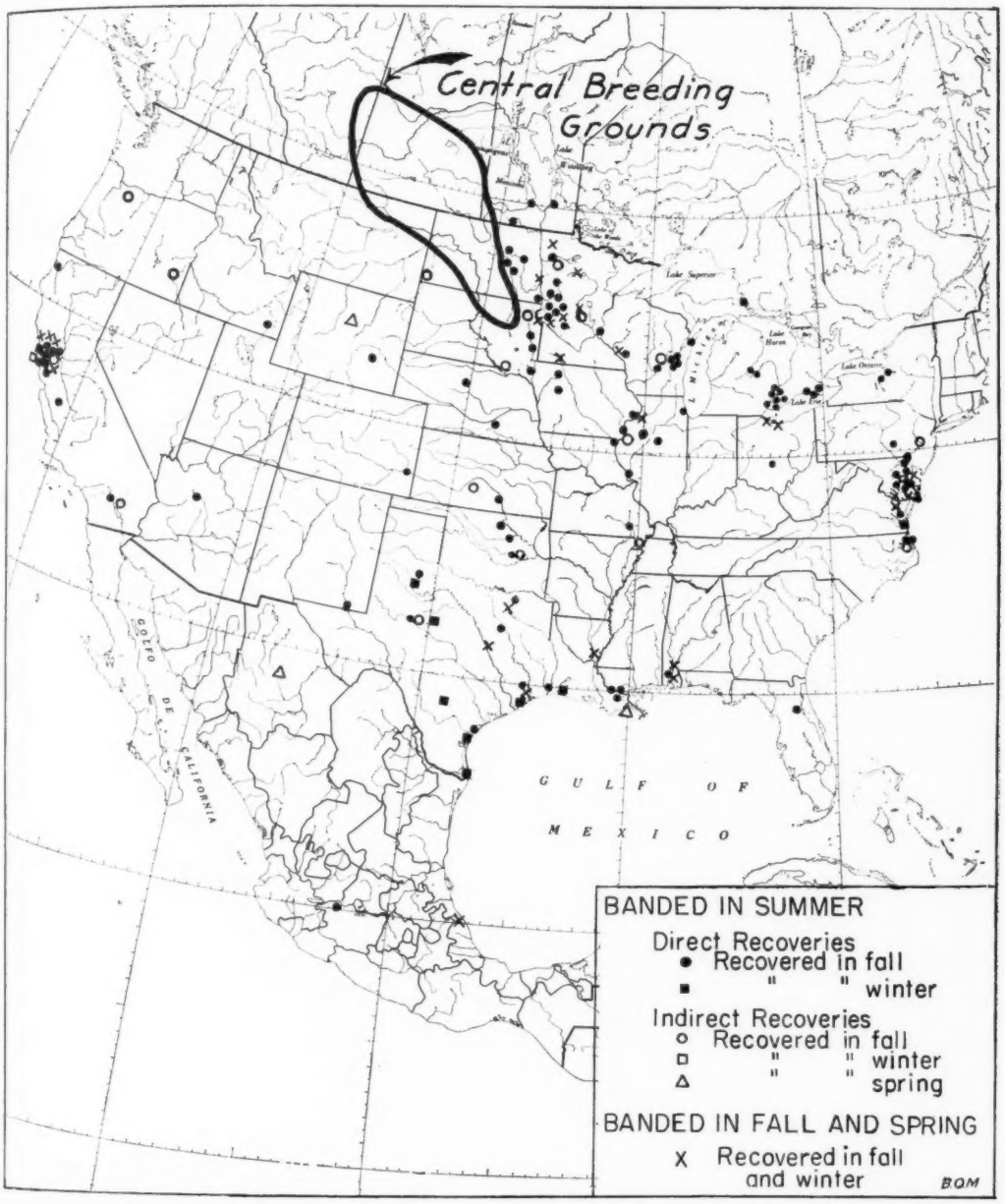

FIG. 5. Distribution of distant recoveries of canvasbacks banded on the central breeding grounds.

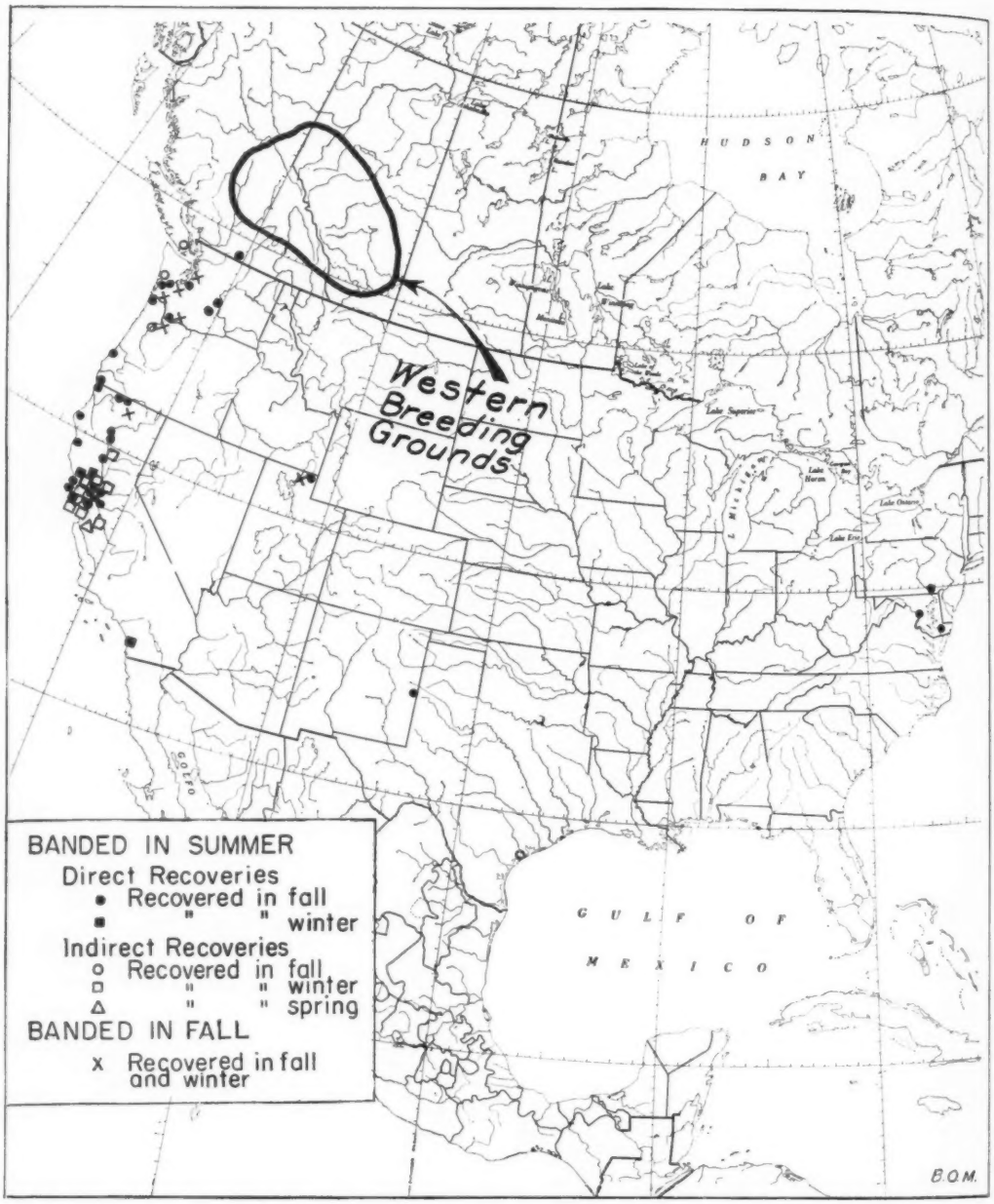

FIG. 6. Distribution of distant recoveries of canvasbacks banded on the western breeding grounds.

the Lake Claire–Athabaska delta area, 5 in the boreal forest area of Alberta, and 2 in the boreal forest area of Saskatchewan. In addition, there were 2 distant recoveries of canvasbacks banded in the fall.

Nearly nine-tenths of the recoveries of birds banded in summer were reported from wintering grounds. Of these, about half were from areas near the Pacific Coast and one-fourth from the Great Lakes and Mid-Atlantic areas. Most of the remainder were reported from Oklahoma, Texas, and Mexico. The recoveries indicate that these birds were widely dispersed among the

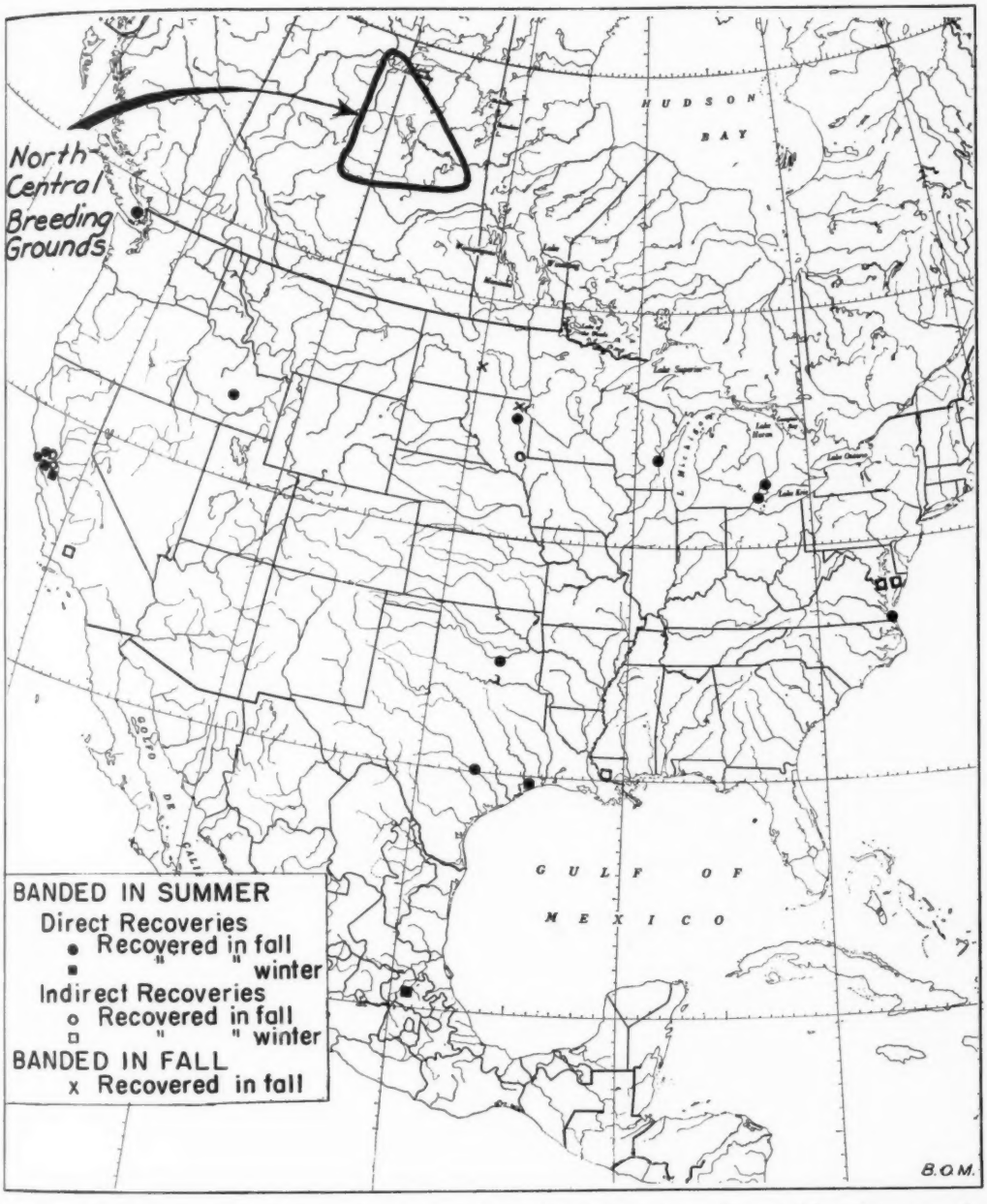

FIG. 7. Distribution of distant recoveries of canvasbacks banded on the north-central breeding grounds.

various migration routes and wintering grounds. However, the greatest concentration occurred on San Francisco Bay.

Alaskan breeding grounds (Fig. 8).—Twenty canvasbacks banded in the summer on the Alaskan breeding grounds were recovered elsewhere, including 9 banded on the Yukon Flats, 9 on the Minto Lakes, and 2 on the Tanana River.

Most of the recoveries were from near the Pacific Coast, while two were from Mid-Atlantic States. The distribution of recoveries suggests that the principal migration route for this population extends

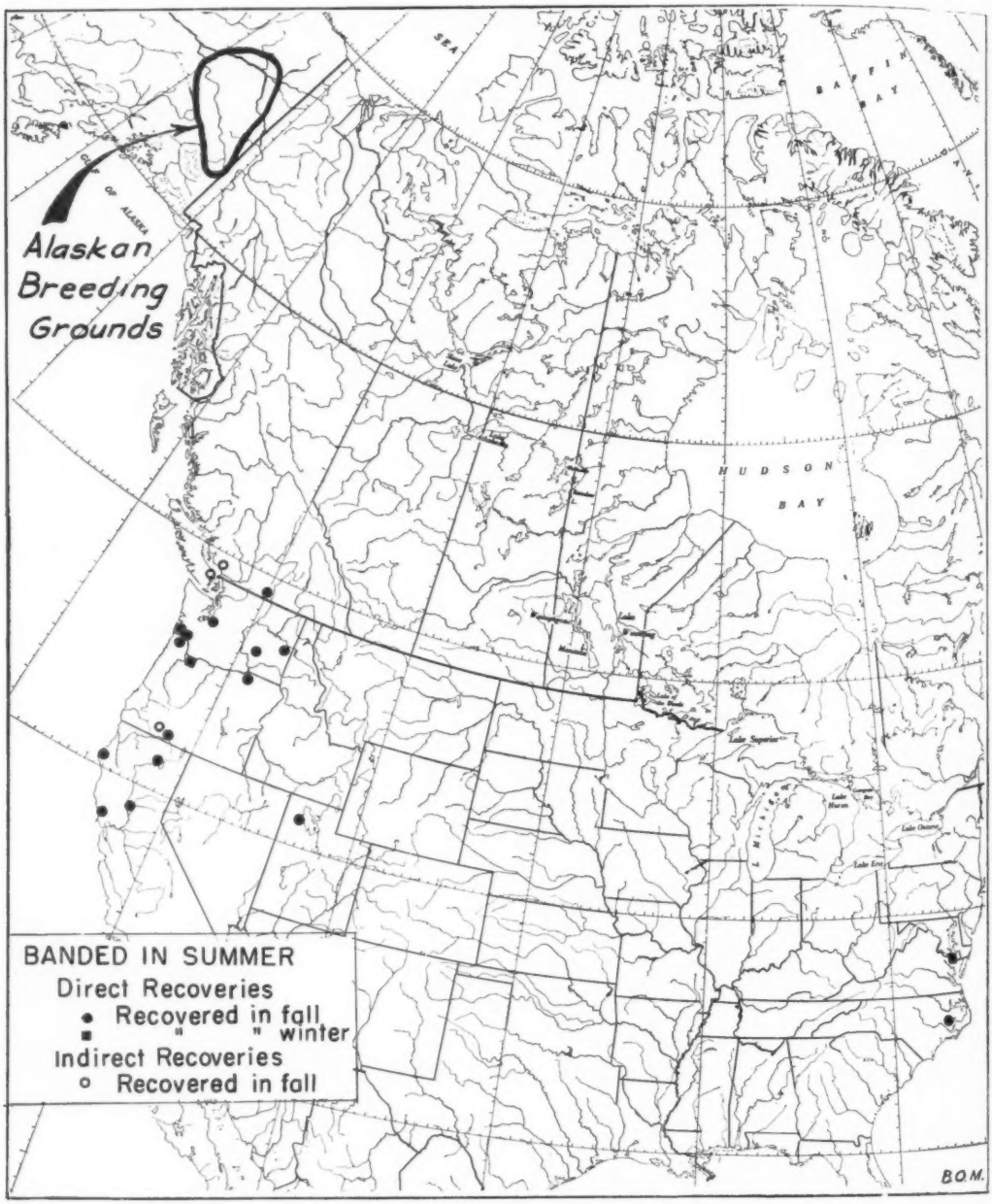

FIG. 8. Distribution of distant recoveries of canvasbacks banded on the Alaskan breeding grounds.

through southern British Columbia, Washington, Oregon, and northern California.

Southeastern Idaho and Lake Malheur, Oregon.—Although there has been only one recovery from bandings in the summer, the region is included here because there were 58 recoveries of birds banded as migrants. Twenty-seven spring and fall migrants from southeastern Idaho and 31 from Lake Malheur, Oregon, were recovered outside of the banding areas. About two-thirds of the birds from each area were recovered in or near San Francisco Bay, showing that the bay is of major importance as a wintering

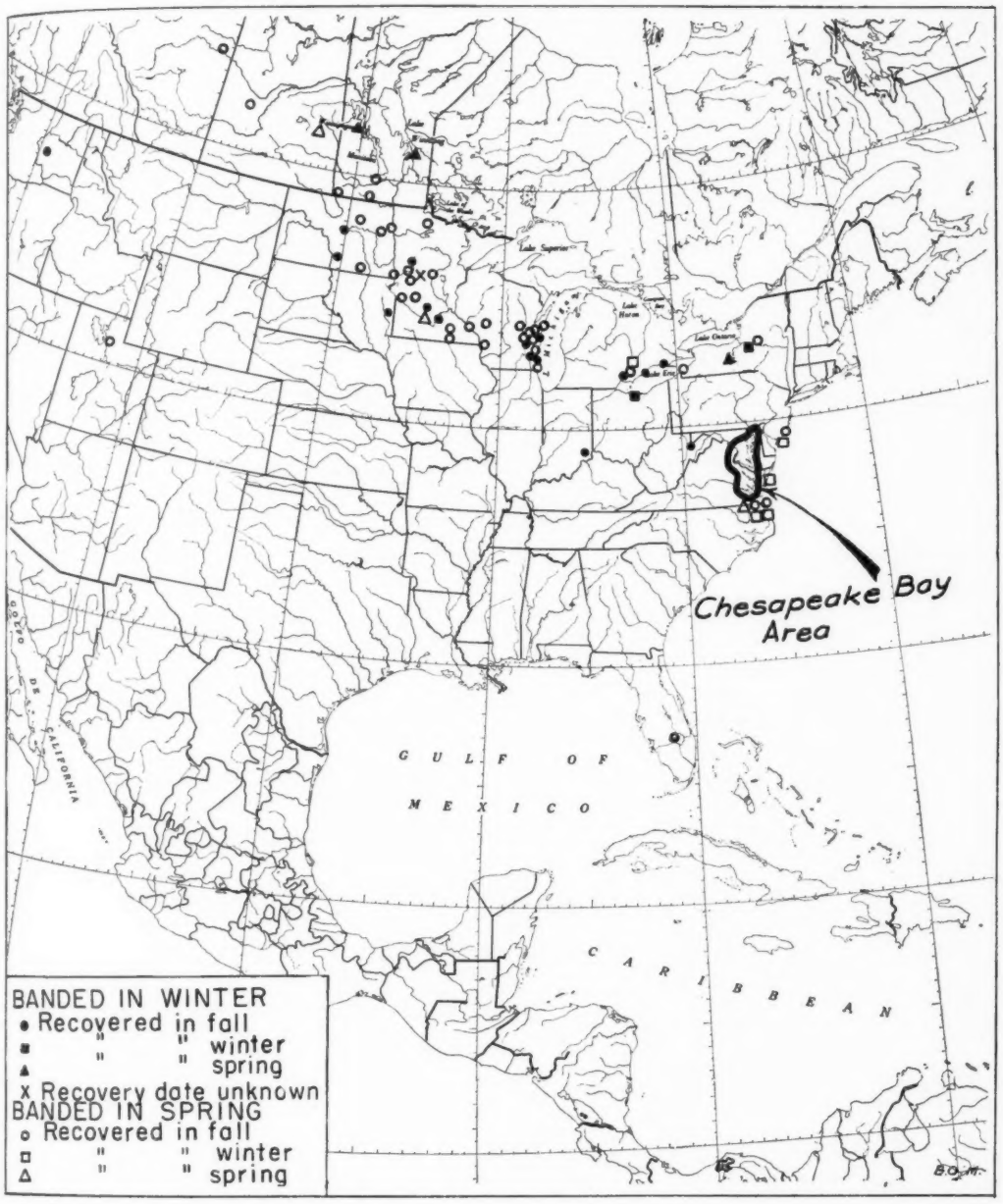

FIG. 9. Distribution of distant recoveries of canvasbacks banded in the Chesapeake Bay area.

ground for these migrant populations. Two of the Idaho birds moved in a more southerly direction; one was taken in southern Arizona and the other in Chihuahua, Mexico. Other records of interest from this general region include one bird banded in southeastern Idaho in summer, and one banded at Ruby Lake, Nevada, in fall. Both were recovered on San Francisco Bay.

MOVEMENTS OF MIGRANT AND WINTERING CANVASBACKS BANDED ON WINTERING AREAS

Further information concerning migratory movements of canvasbacks was derived

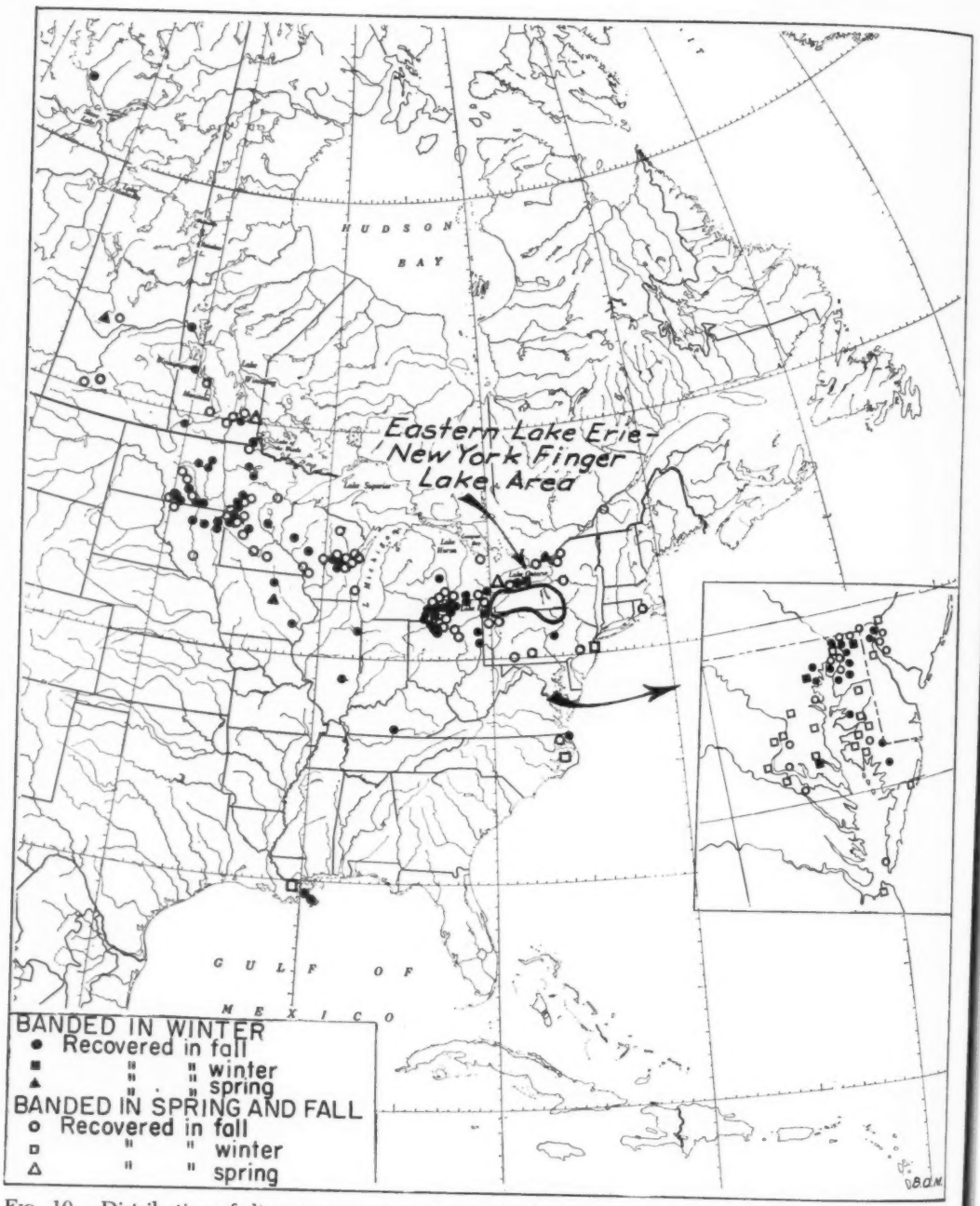

FIG. 10. Distribution of distant recoveries of canvasbacks banded in the eastern Lake Erie–New York Finger Lakes area.

from an analysis of distant recoveries of birds banded during the winter, spring, and fall at several banding stations located on the wintering grounds. The seasons are defined as in the previous section concerning migratory movements from the breeding grounds.

Mid-Atlantic States.—Sixty-seven canvasbacks banded in the Chesapeake Bay area were recovered elsewhere (Fig. 9). These

included 22 banded in winter and 45 banded in spring. The distribution of recoveries from winter and spring banding was similar, except that all recoveries reported from other localities along the Atlantic Coast were of birds that had been banded in the spring. Apparently the principal migration route of the Chesapeake population extends from southern Saskatchewan, southern Manitoba, and eastern North Dakota, through Minnesota and Wisconsin and the eastern Great Lakes to Chesapeake Bay.

Seventeen canvasbacks banded in the coastal strip extending from Long Island to Delaware Bay were recovered in other areas. Nine of these were taken in Chesapeake Bay and the others were taken along the migration route through South Dakota, Minnesota, Wisconsin, and the eastern Great Lakes.

South-Atlantic States.—A total of 21 canvasbacks banded in the sea-island coastal section of South Carolina and small adjacent coastal areas of North Carolina and Georgia was recovered elsewhere. The recoveries were made along a rather narrow route extending from southeastern Manitoba through Minnesota, Wisconsin, and the Detroit River–Lake St. Clair area to Chesapeake Bay, and thence southward along the coast. Apparently these birds followed the same migration route to the Atlantic Coast as did the Chesapeake Bay population.

Eastern Lake Erie–New York Finger Lakes area (Fig. 10).—Of the 179 canvasbacks banded in this area and recovered elsewhere, 81 were banded in winter and 98 in spring and fall. The pattern of distribution of recoveries of birds banded here in

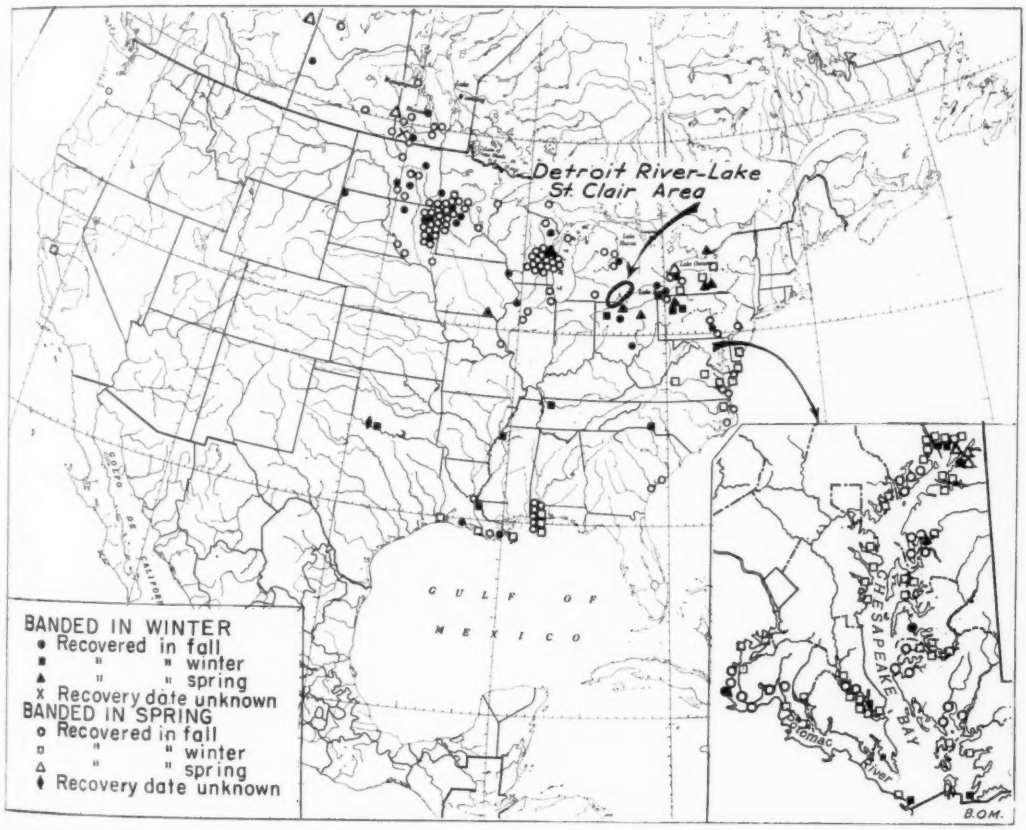

FIG. 11. Distribution of distant recoveries of canvasbacks banded in the Detroit River–Lake St. Clair area.

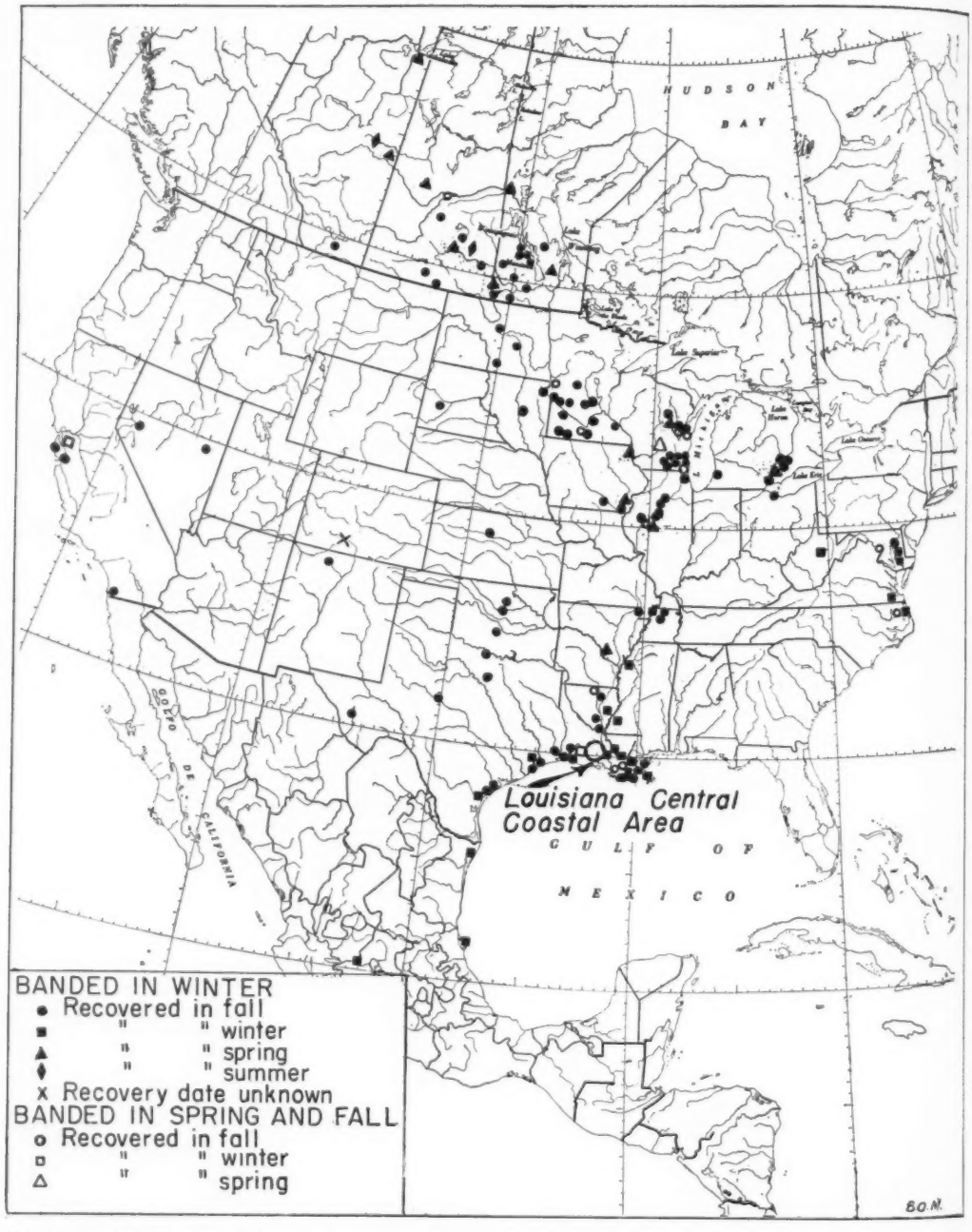

FIG. 12. Distribution of distant recoveries of canvasbacks banded in the Louisiana central coastal area.

spring and fall was similar to that of birds banded in winter, except that a higher proportion of the spring- and fall-banded birds was taken in Chesapeake Bay. This is not surprising since some of the birds banded in the spring and fall probably were migrants that wintered on Chesapeake Bay. A considerable amount of shifting of wintering birds between these two areas probably occurs, for 15 canvasbacks that were banded

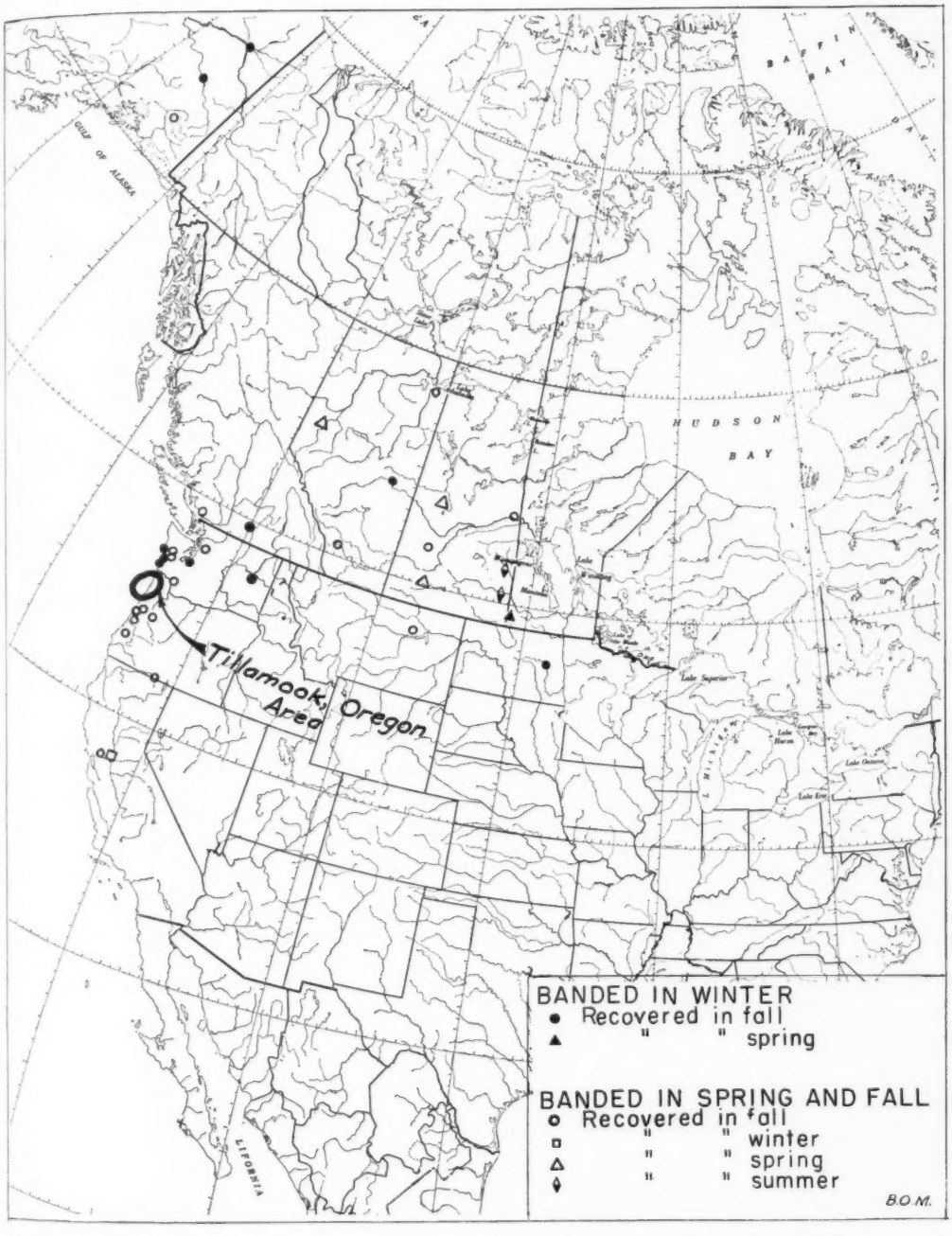

FIG. 13. Distribution of distant recoveries of canvasbacks banded in the Tillamook, Oregon, area.

in winter in the New York area were recovered later on Chesapeake Bay. The principal migration routes taken by canvasbacks from these two areas are nearly identical.

Detroit River–Lake St. Clair area (Fig. 11).—The number of canvasbacks banded in the Detroit River–Lake St. Clair area and recovered elsewhere totaled 240. This included 58 birds banded in winter and 182

banded in spring. Approximately one-third of the recoveries were from the Chesapeake Bay area. These included 37 per cent of the spring-banded canvasbacks, and 19 per cent of those banded in winter. This indicates that Chesapeake Bay is of major importance as a wintering ground for canvasbacks migrating through the Detroit River–Lake St. Clair area, and that considerable numbers of wintering birds also shift from the Detroit River–Lake St. Clair area to Chesapeake Bay. Other important concentrations of recoveries were reported from the Lake Winnebago area of Wisconsin, and from the sector where North Dakota, South Dakota, and Minnesota adjoin. The principal migration route of this population apparently extends from southern Saskatchewan and southern Manitoba through eastern North Dakota, northeastern South Dakota, central Minnesota, and central Wisconsin to the Detroit River–Lake St. Clair area, and large numbers apparently continue from there to Chesapeake Bay. A flight of secondary importance extends from the Detroit River–Lake St. Clair area to eastern Lake Erie and the New York Finger Lakes. Another flight apparently branches southward to the coasts of Louisiana and Alabama. It should be pointed out, however, that the data used here are from indirect recoveries; birds recovered on the Gulf Coast may have migrated directly down the Mississippi River in the year of recovery.

Louisiana coast (Fig. 12).—A total of 142 canvasbacks banded in the central coastal area of Louisiana was recovered elsewhere. This included 127 birds banded in winter and 15 banded in spring and fall. The distribution of recoveries suggests that the principal migration route for this population extends in a southeasterly direction from southern Saskatchewan and southern Manitoba through North Dakota, southern Minnesota, and southern Wisconsin, then continues southward along the Mississippi Valley to the coast of Louisiana. Smaller numbers apparently shift their wintering grounds and migrate southward from the Prairie Provinces through the Great Plains to Texas and Mexico. A few also shift into the Pacific coastal and other western regions, and into the eastern Great Lakes and Chesapeake Bay areas.

San Francisco Bay area.—Fourteen canvasbacks banded in the San Francisco Bay area were recovered elsewhere, including 8 birds banded in winter and 6 banded in fall. Winter-banded birds were recovered from widely scattered areas: 2 were from southern Alberta, 1 from central Wyoming, 1 from Michoacan, Mexico, 1 from the Puget Sound area of Washington, 1 from northern California, and 2 from central California. All of the fall-banded birds were recovered in central California.

Oregon coast (Fig. 13).—Thirty-five canvasbacks, banded in the Tillamook area of the Oregon coast, were recovered elsewhere. These birds included 11 banded in winter and 24 banded in spring and fall. The distribution of the recoveries indicates that the interior of Alaska and the northern prairies and parklands are important breeding grounds for canvasbacks wintering in this area. None of the canvasbacks banded in winter was taken farther south, but one-third of those banded in spring and fall were recovered south of Tillamook toward San Francisco Bay. This indicates that many of the spring- and fall-banded birds were migrants, and also that birds wintering in coastal Oregon probably winter consistently in this area. The distribution of recoveries suggests that spring- and fall-banded birds breed mainly on the Canadian prairies and parklands, while winter-banded birds are more closely associated with Alaskan breeding grounds.

PRINCIPAL MIGRATION ROUTES OF THE CANVASBACK

The more important migration routes used by the canvasback can be defined in at least a preliminary, generalized way from the data now available. Most of this information was reviewed in the previous two sections concerning distribution of breeding and wintering populations and migratory movements. These data were used to prepare a diagrammatic map showing the principal migration routes (Fig. 14). The

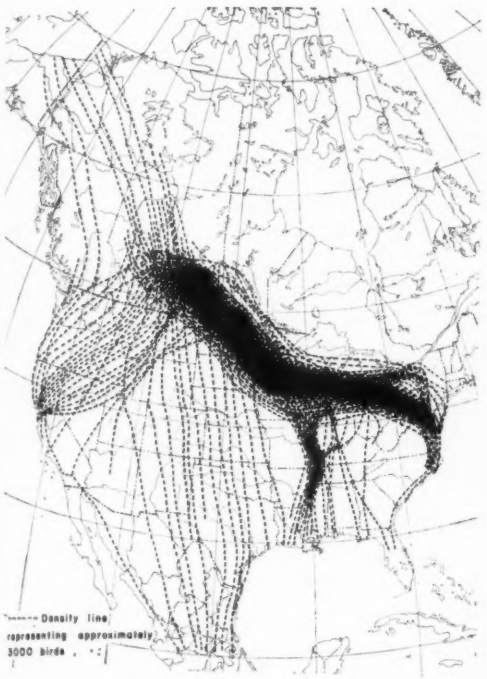

FIG. 14. Diagrammatic map showing principal migration routes of the canvasback.

course and volume of migratory movements were determined as follows: The distribution of recoveries from breeding and wintering areas was used to interpret the course along which the birds moved; the relative numbers of birds moving along the courses were determined by relating each route to the size of the wintering population at its terminus and, in far northern areas, to the size of the breeding population at its beginning. The approximate numbers of canvasbacks that move along the various routes are shown on the map by the dashed lines; each dashed line represents the course followed by approximately 3,000 wintering birds. Along certain areas, traversed by large numbers of birds, the dashed lines merge to form a solid band.

The important primary or trunk route of migrating canvasbacks extends from the prairies and parklands of south-central Canada through the Dakotas, Minnesota, Wisconsin, and the Detroit River–Lake St. Clair area, and then continues across the Appalachian Mountains, and terminates in Chesapeake Bay. A noticeable segment of this flight apparently leaves the trunk route to pass through the eastern Lake Erie–New York Finger Lakes area, before swerving down to Chesapeake Bay. Relatively small numbers of canvasbacks continue from Chesapeake Bay along the coast into the South Atlantic States.

Secondary flights of considerable importance include one that leaves the main trunk route in the vicinity of southern Minnesota and southern Wisconsin and continues down the Mississippi Valley to the Gulf Coast; another that extends from the interior of Alaska, the Prairie Provinces and the Cariboo Parklands of British Columbia to the Pacific coastal area of northern California, Oregon, Washington, and southern British Columbia; and one that extends from the Prairie Provinces through the Great Plains into Texas and Mexico. Certain minor routes occur as deviations or spurs from the principal flights and are also shown on the map.

It is obvious that most migrating canvasbacks pass through more than one of the current administrative flyways as defined by Aldrich, *et al.* (1949:3). For example, the canvasbacks that winter along the Atlantic Coast and comprise the bulk of the continental population migrate through parts of three flyways—the central, Mississippi, and Atlantic. Western wintering populations migrate through parts of two flyways —the central and Pacific. Canvasbacks wintering in the lower Mississippi Valley, and in Texas and Mexico, mingle with both eastern and western populations during part of their journeys.

RELATIONSHIP OF HARVEST AREAS TO BREEDING AND WINTERING CANVASBACK POPULATIONS

The distribution of the hunting kill of canvasbacks from various breeding areas was determined by a study of the distribution of banded birds recovered by shooting. Table 3 shows the proportion of birds recovered in each harvest area that came from each production area. The validity of the data in Table 3 is affected by the many

TABLE 3.—PERCENTAGE DISTRIBUTION OF HUNTING KILL, BASED ON RECOVERIES OF CANVASBACKS BANDED ON VARIOUS BREEDING GROUNDS BETWEEN MAY 21 AND AUGUST 20

Harvest Areas[1]	Breeding Areas							
	Alaska-Yukon	Lake Claire-Athabaska Delta	British Columbia	Alberta	Saskatchewan	Manitoba	North Dakota	South Dakota
North Atlantic States								
New York					1	2	2	4
Pennsylvania			2		1		2	4
Total			*2*		*2*	*2*	*4*	*8*
Mid-Atlantic States								
Maryland	4	6		4	5	18	11	
North Carolina	4				1	2		
Virginia				10	3	4	5	4
Total	*8*	*6*		*14*	*10*	*24*	*16*	*4*
Southeastern States								
Alabama					1			
Florida					1			
Total					*2*			
East-central States								
Ohio					1			4
Tennessee						1		
Total					*1*	*1*		*4*
Great Lakes Area								
Michigan		6			4	5	7	8
Ontario	4			5	4	6	2	8
Wisconsin		6			2	7	5	3
Total	*4*	*12*		*5*	*10*	*18*	*14*	*19*
Western Lake States								
Minnesota					8	11	14	4
North Dakota					6	3	20	15
South Dakota		6			4	5	7	19
Total		*6*			*18*	*19*	*41*	*38*
Midwestern States								
Illinois					1	2	2	
Iowa					2		8	
Missouri					1			4
Total					*4*	*2*	*10*	*4*
Lower Mississippi Valley								
Arkansas					1			
Louisiana					2	2	2	4
Total					*3*	*2*	*2*	*4*
Central Plains States								
Kansas					1	1	2	
Nebraska					2	2		
Oklahoma				5	3		2	
Total				*5*	*6*	*3*	*4*	
Texas								
Total		*12*	*2*		*9*	*3*		*8*
Mexico								
Central Mexico		6			1	1	2	
Northern Mexico								4
Total		*6*			*1*	*1*	*2*	*4*

[1] No recoveries were made from states that are omitted.

(Continued on next page)

TABLE 3.—PERCENTAGE DISTRIBUTION OF HUNTING KILL (CONT'D.)

Harvest Areas[1]	Breeding Areas							
	Alaska-Yukon	Lake Claire-Athabaska Delta	British Columbia	Alberta	Saskatchewan	Manitoba	North Dakota	South Dakota
Arizona–New Mexico								
Arizona					1			
New Mexico				5			2	
Total				*5*	*1*		*2*	
Nevada–Utah								
Nevada				5				
Utah	4			5				
Total	*4*			*10*				
Colorado–Wyoming								
Colorado								4
Wyoming						1		
Total						*1*		*4*
Idaho–Montana								
Idaho		6			1			
Total		*6*			*1*			
California								
Total	*16*	*44*	*51*	*38*	*8*	*2*	*2*	*4*
Northwestern Area								
British Columbia	12	6	24					
Oregon	20		7		1			
Washington	28		13	5		1		
Total	*60*	*6*	*44*	*5*	*1*	*1*		
Prairie Provinces								
Alberta				19				
Manitoba					4	20	2	
Saskatchewan					19	2		
Total				*19*	*23*	*22*	*2*	
Alaska								
Total	8							
Grand Total	*100*	*100*	*100*	*100*	*100*	*100*	*100*	*100*
Total Recoveries	25	16	45	21	135	188	44	26

limitations outlined in the appendix. The areas used were largely political subdivisions, rather than the natural areas described above in connection with migratory movements. Political areas were used primarily because: (1) More accurate population-index values were available for weighting purposes; (2) these were the areas used by the Bureau of Sport Fisheries and Wildlife in forecasting the size of the fall flight; and (3) the use of smaller areas tended to minimize errors caused by an unrepresentative distribution of the banded birds used in this study.

The banded sample consisted of birds captured on the breeding grounds between May 21 and August 20 in the years since 1947. Seventy-four per cent of the recoveries were direct recoveries of birds banded as juveniles, and therefore represented immature birds in the hunting kill; 26 per cent of the recoveries were adult birds, including 16 per cent resulting from indirect recoveries of birds banded as juveniles, and 10 per cent from direct and indirect recoveries of birds banded as adults. The inclusion of indirect recoveries of juveniles and adults, as part of the adult component of the recovery sample, is based on the assumption that most canvasbacks tend to return to the general vicinity of the breeding locality in which they were raised. The ratio of immature

TABLE 4.—PERCENTAGE DISTRIBUTION OF HUNTING KILL AMONG THE ADMINISTRATIVE FLYWAYS, BASED ON RECOVERIES OF CANVASBACKS BANDED ON THE VARIOUS BREEDING GROUNDS BETWEEN MAY 21 AND AUGUST 20

Breeding Areas	Administrative Flyways				
	Pacific	Central	Mississippi	Atlantic	Totals
Alaska–Yukon	89	0	0	11	100
Lake Claire–Athabaska Delta	58	21	14	7	100
British Columbia	95	3	0	3	100
Alberta	69	13	0	18	100
Saskatchewan	15	36	31	18	100
Manitoba	4	21	39	36	100
North Dakota	2	41	35	22	100
South Dakota	13	30	52	5	100

birds to adults in the recovery sample is about 3 to 1.

The kill of canvasbacks banded in southern Saskatchewan was distributed widely over various migration routes and wintering grounds. The heaviest kill occurred in the southern portion of the Prairie Provinces, the part of the Dakotas north and east of the Missouri River, and Minnesota. The greatest part of the kill of Manitoba birds took place along the main trunk route. Almost equal numbers of recoveries were reported from the following areas: (1) southern portion of the Prairie Provinces; (2) the Dakotas and Minnesota; (3) Wisconsin, Michigan and southern Ontario; and (4) the Mid-Atlantic States. Canvasbacks banded in North and South Dakota had similar recovery patterns: The largest kills occurred in the Dakotas and Minnesota; there were also important kills in Wisconsin, Michigan, and southern Ontario. South Dakota apparently differed from North Dakota, however, in that a larger proportion of South Dakota birds was taken in the southern plains and lower Mississippi Valley and smaller numbers were reported from the Mid-Atlantic States. The sample of recoveries from birds banded in southern Alberta and the Lake Claire–Athabaska delta area was very small, but these few indicated that the heaviest kill from both areas took place in California. The harvest of the Lake Claire–Athabaska delta birds differed from the harvest of the southern Alberta birds in that a smaller proportion was taken in Alberta, while a larger proportion was taken in Texas and Mexico. Most of the kill reported from the small British Columbia population was divided between California and the area of British Columbia, Washington, and Oregon. The Alaska–Yukon birds were quite distinct in that nearly two-thirds of the recoveries were from southern British Columbia, Oregon, and Washington; other areas of minor importance included California, the Mid-Atlantic States, and Alaska.

Table 4 shows the distribution of the hunting kill of canvasbacks banded in various breeding areas, as it relates to the four administrative flyways. The population of each breeding area is harvested in more than one flyway. This clearly indicates that the current administrative flyways are not separate, independent zones as far as the populations of this species are concerned.

The distribution of the hunting kill of canvasbacks banded on their wintering areas during the period from December 21 through February 20 is shown in Table 5. Only indirect recoveries were used; consequently, the distribution of recoveries reflects the hunting kill of the adults. There was a difference between the sexes in the distribution of the adult hunting kill. Females sustained a relatively higher kill on breeding areas and early in migration, while males had a relatively heavier kill on wintering grounds. For example, of canvasbacks banded in the Mid-Atlantic States, 42 per cent of the recoveries of females occurred on the breeding grounds or in states traversed early in migration, while only 22

TABLE 5.—PERCENTAGE DISTRIBUTION OF HUNTING KILL, BASED ON INDIRECT RECOVERIES OF CANVASBACKS BANDED BETWEEN DECEMBER 21 AND FEBRUARY 20 ON VARIOUS WINTERING GROUNDS

Harvest Areas[1]	Wintering Areas											
	Mid-Atlantic States (Md.,Va.,N.C.)		New York		Michigan		Louisiana		California		Oregon	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
North Atlantic States												
Connecticut				1								
New Jersey	1		1									
New York	1	4	29	30	1							
Pennsylvania		2	1	3		6						
Total	*2*	*6*	*31*	*34*	*1*	*6*						
Mid-Atlantic States												
Maryland	45	27	18	19	10	12	2					
North Carolina	10	4	1	1	1			2				
Virginia	10	10	3	2	3		1					
Total	*65*	*41*	*22*	*22*	*14*	*12*	*3*	*2*				
Southeastern States												
Alabama			1									
Total			*1*									
East-central States												
Indiana	1						1					
Kentucky				1								
Ohio			1	2	6	3	1					
Tennessee					4		1	2				
Total	*1*		*1*	*3*	*10*	*3*	*3*	*2*				
Great Lakes Area												
Michigan	2	2	7	5	16	13	1	2				
Ontario	5	2	5	6	21	19		2				
Wisconsin	7	4	3	6	3	13	6	10				
Total	*14*	*8*	*15*	*17*	*40*	*45*	*7*	*14*				
Western Lake States												
Minnesota	8	17	8	12	7	13	5	10				
North Dakota	4	6	5	5	4	10	1	2			6	
South Dakota		8	2	4	6	3	2					
Total	*12*	*31*	*15*	*21*	*17*	*26*	*8*	*12*			*6*	
Midwestern States												
Iowa	1				1							
Illinois		2	3		1		4	5				
Total	*1*	*2*	*3*		*2*		*4*	*5*				
Lower Miss. Valley												
Louisiana		2	1	1	4		54	40				
Mississippi					1							
Total		*2*	*1*	*1*	*5*		*54*	*40*				
Central Plains States												
Kansas								2				
Oklahoma					1		1	3				
Total					*1*		*1*	*5*				
Texas												
Total					*1*		*4*	*6*				
Mexico												
Central Mexico							1	2		9		
Northern Mexico							1					
Total							*2*	*2*		*9*		

(Continued on next page)

TABLE 5.—PERCENTAGE DISTRIBUTION OF HUNTING KILL (CONT'D.)

Harvest Areas[1]	Wintering Areas											
	Mid-Atlantic States (Md.,Va.,N.C.)		New York		Michigan		Louisiana		California		Oregon	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Arizona–New Mexico												
New Mexico							1				6	
Total							*1*				*6*	
Nevada–Utah												
Nevada							1	2				
Total							*1*	*2*				
Colorado–Wyoming												
Wyoming									8			
Total									*8*			
Idaho–Montana												
Idaho	1											
Montana	1											
Total	*2*											
California												
Total							*1*	*3*	*85*	*82*		
Northwestern Area												
British Columbia											6	
Oregon											50	83
Washington	1								8		31	
Total	*1*								*8*		*87*	*83*
Prairie Provinces												
Alberta							2			9	6	
Manitoba		6	5	4	1	6	4	6				
Saskatchewan	1	2	1	1	3		2	3				
Total	*1*	*8*	*6*	*5*	*4*	*6*	*8*	*9*		*9*	*6*	
Alaska												
Total												*17*
Grand Total	100	100	100	100	100	100	100	100	100	100	100	100
Total Recoveries	84	48	271	107	68	31	129	62	13	11	16	6

[1] No recoveries occurred in harvest areas not listed.

per cent of the male kill occurred in these areas. In contrast, 43 per cent of the female kill and 71 per cent of the male kill occurred on wintering areas. Both Hochbaum (1944) and Smith (1946) present field observations indicating that adult females are more heavily shot than adult males on breeding grounds and early in migration. The probable reason for the difference between the sexes in the distribution of the hunting kill is that adult males migrate earlier and/or faster than adult females and consequently are exposed to less shooting pressure on the breeding grounds and early in migration. Unlike the situation with adults, summer banding records indicated that the kill pattern of male and female immature canvasbacks was similar.

The pattern of the hunting kill of canvasbacks banded in California and Oregon in winter differed somewhat from that of other wintering populations, for the kill was more concentrated near the wintering areas where the banding was done. In the other four areas, higher proportions of the recoveries were made along the migration routes and on the breeding grounds. Birds wintering in Oregon and California apparently migrate through areas of light hunting pressure while other wintering populations are shot more heavily during migration. Canvasbacks banded in New York and Michigan

apparently did not use the same wintering grounds consistently, and consequently a larger proportion of recoveries was from areas other than those in which the birds were banded.

There was an apparent difference in the pattern of kill distribution of summer-banded and winter-banded canvasbacks. A higher proportion of winter-banded birds was taken on wintering grounds while a higher proportion of summer-banded birds was taken in breeding areas and early in migration. The reason for this difference was that 76 per cent of the summer-banded birds were killed as juveniles, while recoveries from winter bandings reflect solely the kill of adults. To see if this was true, the recovery records of birds banded in Saskatchewan and Manitoba in summer were compared with recovery records of certain winter-banded birds. Recoveries of adults banded in Saskatchewan and Manitoba (either birds banded as adults or indirect recoveries of juveniles) were compared with recoveries of immature birds banded in the same area and with recoveries of adult females banded during winter in the Mid-Atlantic States (Table 6). Adult females were used because 70 per cent of the adult recoveries from summer bandings were females. The results of these comparisons may be summarized as follows: (1) Juveniles were killed on the breeding grounds to a larger extent than were adults; (2) adults were killed on the wintering grounds in relatively greater numbers than were juveniles; (3) summer-banded birds recovered as adults showed a proportionately greater kill on the breeding grounds than winter-banded adults. When the above differences were tested statistically, it was found that in all instances the probability that they were due to chance was between 0.20 and 0.05.

A possible explanation for the difference between the kill distribution of adults banded on the breeding grounds and those banded on wintering areas is that all summer-banded birds were captured in easily accessible parts of the breeding range. Consequently, it is reasonable to suppose that they would be subjected to a heavier breeding-ground shooting pressure than a winter population, which also includes birds that breed in more inaccessible areas.

BREEDING-GROUND DERIVATION OF THE HUNTING KILL IN VARIOUS HARVEST AREAS

Information on the distribution and breeding-ground derivation of the hunting kill, discussed in this section and the one following, is based on weighted band recoveries. In order to use banding data in this manner, two conditions must be met:

1) All significant parts of the population must be represented by a banded sample.

2) The relative size of each part of the population represented by a banded sample must be known.

The first condition was met fairly well by summer bandings, since at least some birds were banded in all important production areas. Areas not included by banded samples were Minnesota, Montana, and the other western states, and also the Mackenzie River drainage north from the Alberta line.

TABLE 6.—PERCENTAGE DISTRIBUTION OF CANVASBACK KILL BY AGE GROUPS

Age Group	Immature	Adults	
Season of Banding	Summer	Summer	Winter
Location of Banding	Manitoba and Saskatchewan	Manitoba and Saskatchewan	Mid-Atlantic States
Number of Recoveries	224	86	48
Harvest Areas	*Percentages*		
Prairie Provinces	26	15	8
Migration Routes	40	40	46
Wintering Areas	34	45	46
Totals	100	100	100

TABLE 7.—BREEDING-GROUND DERIVATION OF CANVASBACK KILL IN VARIOUS HARVEST AREAS
(Each number represents the percentage of the total kill in each harvest area that relates to each breeding ground)

Harvest Areas	Breeding Ground								
	Alaska–Yukon	Lake Claire–Athabaska Delta	British Columbia	Alberta	Saskatchewan	Manitoba	North Dakota	South Dakota	Totals
North Atlantic Region (Conn., Mass., N.J., N.Y., Pa., R.I.)	0	0	+	0	68	9	19	3	100
Mid-Atlantic Region (Del., Md., N.C., Va.,W.Va.)	4	1	0	16	49	18	11	+	100
Southeastern Region (Ala., Fla., Ga., S.C.)	0	0	0	0	100	0	0	0	100
East-central Region (Ind., Ky., Ohio, Tenn.)	0	0	0	0	72	23	0	5	100
Great Lakes Region (Mich., Ont., Wis.)	2	2	0	6	61	15	11	2	100
Western Lake Region (Minn., N.Dak., S.Dak.)	0	1	0	0	66	10	21	2	100
Midwestern Region (Iowa, Ill., Mo.)	0	0	0	0	73	5	21	1	100
Lower Mississippi Valley (Ark., La., Miss.)	0	0	0	0	81	9	9	1	100
Central Plains Region (Kans., Nebr., Okla.)	0	0	0	13	74	5	8	0	100
Texas	0	4	+	0	90	5	0	1	100
Mexico	0	9	0	0	67	7	14	2	100
Prairie Provinces (Alta., Man., Sask.)	0	0	0	14	75	10	1	0	100
Northern Montane Region (Colo., Idaho, Mont., Wyo.)	0	18	0	0	70	7	0	5	100
Southern Montane Region (Ariz., Nev., N.Mex., Utah)	7	0	0	69	16	0	7	0	100
California	7	7	2	42	40	1	2	+	100
Northwestern Region (B.C., Oreg., Wash.)	69	3	4	14	10	1	0	0	100
Total Recoveries	25	16	45	21	135	188	44	26	

These areas, although large, have low population densities and contain probably less than 10 per cent of the total breeding population of canvasbacks.

Information required to fulfill the second condition was obtained from the breeding-ground surveys. The breeding-ground surveys give data on the numbers of breeding pairs in the spring. It is necessary to assume that in all areas under consideration the size of the breeding population bears the same relationship to that of the fall flight.

The breeding-ground derivation of the hunting kill in various harvest areas was estimated as follows: The number of recoveries in each harvest area of birds that were banded between May 21 and August 20 in each production area were given weighted values. The weighting factors were based on index values for the breeding population for the four-year period, 1953–56. The kill-index values thus obtained show the contribution from each breeding area to the kill in each harvest area (Table 7).

The assumptions made and the validity of the data are discussed in the appendix.

The prairie and parkland region within Saskatchewan, Manitoba, and the Dakotas contributed the great majority of canvasbacks shot throughout the area east of the Rocky Mountains. Saskatchewan alone produced most of them. Birds produced in Manitoba were relatively more important in the kill of the north-central and eastern harvest areas (i.e., Wisconsin, Michigan, southern Ontario, and the Mid-Atlantic States) than they were in areas to the south and west. Most of the birds shot in the Southwestern States (Arizona, Nevada, New Mexico, and Utah) were produced in Alberta. Canvasbacks killed in California were produced in all areas; estimates showed, however, that the largest contributions were from Alberta (42 per cent) and Saskatchewan (40 per cent). More than two-thirds of the birds killed in southern British Columbia, Washington, and Oregon were produced in the Alaska–Yukon breeding area.

DISTRIBUTION OF THE TOTAL HUNTING KILL

The estimated distribution of the total canvasback kill was based on weighted recoveries from summer banding. The procedures followed were the same as those used to estimate the breeding-ground derivation of the kill in each harvest area. A total-kill index for each harvest area was obtained by adding together the weighted values of the recoveries from all production areas contributing to that kill. The resulting kill-index values for all harvest areas were then compared in order to determine the distribution of the total kill.

The estimated proportions of the total kill from various harvest areas are given in Table 8 and Fig. 15. They show that approximately 75 per cent of the total kill occurred within the United States, 24 per cent in Canada, and 1 per cent in Mexico. In Canada most of the kill took place in the Prairie Provinces (19 per cent of total) and southern Ontario (4 per cent). Relatively small kills also were estimated for British Columbia (1 per cent) and Alaska.

TABLE 8.—PERCENTAGE DISTRIBUTION OF TOTAL CANVASBACK KILL, BASED ON WEIGHTED BAND RECOVERIES

Harvest Area	Kill-index Value	Per Cent	Harvest Area	Kill-index Value	Per Cent[1]
California	42,615	12	North Carolina	4,654	1
Southern Saskatchewan	41,112	12	New York	4,545	1
			Central Mexico	4,509	1
Minnesota	24,657	7	Illinois	4,432	1
Maryland	23,145	7	Alabama	3,112	1
			Utah	2,952	1
Texas	20,721	6	New Mexico	2,894	1
North Dakota	19,696	6	British Columbia	2,890	1
			Kansas	2,384	1
Southern Manitoba	14,512	4	Pennsylvania	2,362	1
Michigan	13,435	4	Nevada	2,230	1
Southern Ontario	13,426	4	Ohio	1,997	1
Virginia	13,273	4	Idaho	1,961	1
South Dakota	12,218	4			
			Missouri	1,669	+
Oklahoma	9,118	3	Arkansas	1,556	+
Southern Alberta	8,920	3	Arizona	1,556	+
			Florida	1,556	+
Wisconsin	8,646	2	Alaska	1,444	+
Washington	7,622	2	Tennessee	164	+
Iowa	6,660	2	Wyoming	164	+
Louisiana	6,101	2	Colorado	113	+
Nebraska	5,324	2	Northern Mexico	113	+
Oregon	5,253	2	*Totals*	*345,711*	*100*

[1] + indicates percentage of 0.5 or less.

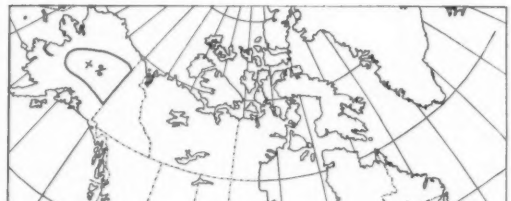

FIG. 15. Distribution of total canvasback kill (derived from weighted recoveries of birds banded during the breeding season).

Additional information on the distribution of the canvasback kill in the United States was obtained from respondents to the mail survey of waterfowl hunters, which is conducted annually by the Bureau of Sport Fisheries and Wildlife. This survey was designed and routinely analyzed to estimate the kill on the basis of four areas, the Pacific, Central, Mississippi, and Atlantic administrative flyways. For the present study the routine survey data were subdivided further in order to obtain kill estimates for the same harvest areas that were referred to earlier in estimating the distribution of the kill from band-recovery data.

Estimates of the kill distribution of canvasbacks in the United States thus were obtained from two independent sources (banding data and the hunter-kill mail survey). These data are presented in Table 9. The heaviest kills occurred in the western lakes region (Minnesota, North Dakota, and South Dakota), Great Lakes region (Michigan and Wisconsin), Mid-Atlantic region

TABLE 9.—PERCENTAGE DISTRIBUTION OF CANVASBACK KILL WITHIN THE UNITED STATES

Harvest Areas	Based on 1953–56 Hunter-kill Surveys	Based on Weighted Band Recoveries
North Atlantic Region (Conn., Mass., N.J., N.Y., Pa., R.I.)	3.2	2.7
Mid-Atlantic Region (Del., Md., N.C., Va., W.Va.)	13.8	15.9
Southeastern Region (Ala., Fla., Ga., S.C.)	1.8	1.8
East-central Region (Ind., Ky., Ohio, Tenn.)	1.3	0.8
Great Lakes Region (Mich., Wis.)	16.8	8.5
Western Lakes Region (Minn., N.Dak., S.Dak.)	16.5	21.9
Midwestern Region (Iowa, Ill., Mo.)	3.4	4.9
Lower Mississippi Valley (Ark., La., Miss.)	4.9	3.0
Central Plains Region (Kans., Nebr., Okla.)	4.9	6.5
Texas	10.0	8.0
Northern Montane Region (Colo., Idaho, Mont., Wyo.)	3.8	0.9
Southern Montane Region (Ariz., Nev., N.Mex., Utah)	2.2	3.7
California	12.7	16.5
Northwestern Region (Oreg., Wash.)	4.4	5.0
Totals	100.0	100.0

(chiefly Maryland, North Carolina, and Virginia), and California. A fairly large kill also occurred in Texas, while relatively small numbers of canvasbacks were shot in other harvest areas.

Since both methods had limitations, it is noteworthy that the estimates were in general agreement. The greatest discrepancy between them was in the estimates for the relatively unimportant area comprising Montana, Wyoming, Idaho, and Colorado. The hunter-kill survey indicated that 3.8 per cent of the canvasbacks killed in the United States were shot in this area, while banding data gave an estimated kill of only 0.9 per cent. Part of this discrepancy probably was caused by the fact that the production within this breeding area was not represented by a banded sample. In effect, the banding data indicated only the kill of birds produced outside the area. In contrast, the hunter-kill survey included the kill of all canvasbacks and therefore yielded a larger estimated kill.

SUMMARY

Canvasbacks were found breeding chiefly in the Interior Plains of west-central Canada and adjacent portions of the United States. Local populations also occurred in the interior of Alaska, northern Yukon, southern British Columbia, and in the northern Rocky Mountains and intermontane areas of the western United States. The major part of the population was found in the aspen parklands and the mixed- and tall-grass prairies of the Prairie Provinces and the Dakotas.

Wintering populations of canvasbacks were found chiefly on the bays and estuaries of the Atlantic, Pacific, and Gulf coasts of the United States and Mexico; and on the larger rivers, lakes, and reservoirs of the southern Great Lakes area, the lower Mississippi Valley, and central Mexico. According to average estimated populations, based on January surveys for the period 1952–56, about four-fifths of the wintering canvasbacks were found in the eastern third of the United States (including adjacent areas in southeastern Ontario), and about one-fifth in the western United States and Mexico. The outstanding concentrations occurred in the Chesapeake Bay area [maximum estimate of 420,000 in 1954] and account for about half the total continental population. Other important concentrations were found in the San Francisco Bay area, in the Detroit River–Lake St. Clair area, on the Mexican central plateau, and in the Mississippi Valley coastal area. Results of January survey counts suggest that partial shifts in wintering populations occasionally took place between the Mississippi Valley and Great Lakes regions and between the Mississippi Valley and Mid-Atlantic regions.

The distribution of 381 recoveries of canvasbacks banded in five breeding areas was examined to determine migration routes and wintering areas. It was found that the eastern wintering areas were most important to populations produced in the eastern breeding grounds, while most of the birds produced in the western breeding grounds wintered on or near the Pacific Coast. Large numbers of canvasbacks from the central breeding grounds wintered in all of the more important wintering areas. Relationships between breeding grounds and wintering areas were also established for the more northern breeding areas.

The course and relative importance of the migration routes of the canvasback were determined. The greatest numbers of birds pass along a primary or trunk route that extends from the prairies and parklands of south-central Canada through the Dakotas, Minnesota, Wisconsin, and Michigan, and then continues southeast, to terminate in the Mid-Atlantic States, principally in Chesapeake Bay. Other secondary flight routes extend from the breeding grounds to the Pacific Coast, the Gulf Coast, Mexico, and other areas.

The distribution of the canvasback hunting kill throughout North America was based on weighted recoveries of banded birds. An estimated 75 per cent of the kill occurred in the United States, 24 per cent in Canada, and 1 per cent in Mexico. The Canadian kill occurred almost entirely in the southern Prairie Provinces and southern Ontario. Within the United States the

largest kill took place in California, Minnesota, Maryland, Texas, and North Dakota. The distribution of the kill of canvasbacks using various production and wintering areas was also determined. Most of the kill from the important eastern and central breeding grounds and eastern wintering areas occurred at certain concentration points along the primary trunk route in Saskatchewan, Manitoba, the Dakotas, Minnesota, Wisconsin, Michigan, Maryland, and Virginia. California was the outstanding harvest area for birds wintering and breeding in more western areas. For each harvest area, the relative importance of the contribution from each production area was determined. In most areas, the production from Saskatchewan was most important.

APPENDIX

In the present study of the canvasback, banding data were used in conjunction with population data to obtain information relating to the entire continental population. In order to do this, it was necessary to use sources of information and methods of analysis that had not been described previously. An evaluation of the reliability of the results also requires an explanation of the nature of the basic data and the methods of interpretation. For these reasons, the survey procedures, the limitations of the data, and the basic assumptions made in their analysis are discussed in detail in this appendix. Also, it is intended that these discussions will be referred to in future studies. Descriptions of some of the procedures followed have been included in various issues of *Special Scientific Report—Wildlife* (U.S. Fish and Wildlife Service). While these descriptions were adequate to meet the needs of the reports involved, they were not sufficiently detailed for the present treatment.

The Breeding-ground Survey

The breeding-ground survey is designed to obtain data to use in predicting annual variations in the size of the fall flight of ducks along the four administrative flyways. These data are considered in setting hunting regulations. They are gathered and analyzed using Canadian provinces as areas of reference so that the information obtained may be used also by the provinces in setting regulations. The survey is designed to establish an index to the probable size of the fall flight of all ducks from each province. This index is then allocated to the four flyways on the basis of probable fall movements, as determined by banding data. The procedure for forecasting the flight to each flyway is described by Crissey (1957).

The breeding-ground survey is designed so that the sampling error of the total duck index for each province would be less than 20 per cent at the 0.05 probability level. Whenever the sampling error has been estimated following a survey, it has been found to be considerably lower than this figure.

To increase the efficiency of surveys, the waterfowl-production area was divided into smaller areas referred to as strata. Strata were established in each province on the basis of the expected waterfowl-population density, the variability of the population and, to some extent, the major habitat types, so that an optimum allocation of sampling could be determined.

The survey is conducted from aircraft flying 100 to 200 feet above the ground along linear routes or "transects." The transects are further divided into segments 18 miles in length, so that studies of variability may be made. A survey crew consists of one man acting as a pilot–navigator–observer, and another man as an observer. Each person records data from a strip ⅛ mile wide on his side of the aircraft. Whenever possible, waterfowl are recorded by species as "pairs," "lone drakes," or "groups of mixed sexes." When identification is not possible, the birds are recorded as a certain number "unidentified."

In analyzing the data, it is assumed that each drake on a breeding area has a hen, either with him or on the nest and invisible to the observers. These unseen hens are included in the final index value. In groups composed of both sexes, a hen is not added for each drake; instead the total count is used. These mixed groups of birds make up only a small portion of the canvasback population during the breeding season. The birds recorded as "unidentified" are allocated as drakes or hens, according to the sex ratio of the "identified" birds. The calculated number of drakes "unidentified" is allocated to the various species in proportion to the occurrence of these species in the "identified" group. A hen is added for each drake in order to arrive at a population index for the sample. These data are then expanded to a population index for the entire stratum.

On the Canadian prairies, waterfowl are often so numerous that it is necessary to use dictaphones to record them. On northern surveys over forest and tundra, waterfowl are more widely scattered and observations are entered directly onto record forms. Surveys in the prairies and parklands are conducted with the Piper "Super-cub," a tandem two-seater flying from 75 to 100 miles per hour. One Cessna "170," a four-seater with the crew sitting side by side, and flying about 100 miles per hour, is used in Alberta. Surveys beyond the prairies and parklands are conducted with Grumman "Goose" and "Widgeon" amphibians flying about 120 miles per hour, with the two crew members side by side.

In the present paper, the breeding-ground survey data were used for two purposes: (1) to show the relative abundance of the canvasback within its breeding range; and (2) to derive weighting factors for use in the analysis of band recoveries. The accuracy of data from the breeding-ground survey is influenced both by sampling errors resulting from the variability of the populations involved, and by bias errors in the observations.

Since the data are put to more detailed use than was the original intention when the survey was designed, sampling errors are not the same as for the total ducks in a province. The canvasback made up only 3.13 per cent of the 1955 index for southern Saskatchewan. Furthermore, data in Fig. 1 are used to indicate the population of 18-mile segments rather than of entire provinces.

The sampling error of the canvasback breeding-population index for 1955 in southern Saskatchewan was found to be ± 6 per cent at the 0.05 probability level. This is only a rough estimate, owing both to the skewness of the data and to the difficulty of allocating canvasbacks from the unidentified portion of the population. Skewness was reduced by a square-root transformation of the data. The problem of the "unidentified" was more difficult. The canvasbacks identified and recorded are undoubtedly much more variable in distribution than the true canvasback population. Furthermore, a correction of the "unidentified," on the basis of the canvasbacks observed on each segment, would not eliminate this problem because a segment that had many ducks, but none identified, would then appear to be without canvasbacks. The best compromise seemed to be to determine the percentage of canvasback drakes among all identified ducks in each stratum and then apply this factor to the unidentified birds of each segment. Although this probably resulted in data closest to the true facts, it minimized the estimated sampling error.

Confidence limits were estimated by standard statistical procedures. The variance estimate for the stratified sample was obtained by formula 5.11 in Cochran (1953:72). Sampling-error estimates also were made for the total population of all species of ducks in order to furnish a standard for comparison with the variability of the canvasback count. It was found that the confidence limits for the estimated total duck population were only slightly narrower than those for the canvasback. Therefore, if the variability of the canvasback data was not excessively minimized by the manner of treating the unidentified birds, it appears that the distribution of canvasbacks is only slightly more variable than that of the total duck population. It can be concluded that, on a provincial basis, sampling error in the data recorded on aerial breeding-pair surveys is not an important problem. However, data from individual 18-mile segments may be subject to considerable error.

Bias errors are much more important and some potential sources are listed below:

1) The estimation of transect width may be inaccurate. Accuracy depends to a large extent on the observer's ability to define the ⅛-mile-wide strip on which observations are made. Throughout much of the prairie and parkland habitat this can be accomplished by constantly checking the spacing of telephone poles along roads that follow most section lines. In open rangeland and in far northern areas, where roads and telephone poles are scarce, the problem of estimating transect width becomes more acute.

2) Weather conditions can influence the counts. High winds and cloud cover influence the visibility of the birds, both by modifying their activity and by affecting the observer's ability to see. Time of day is also important, as shown by Smith (1956, 1957). Winds generally rise toward midday, while poor light occurs most often in the early morning and evening.

3) Over broad areas, variations in water levels and vegetative cover can affect the percentage of the birds seen (Smith, *ibid.*). Low water levels may leave open mud flats around the margins of water areas and increase visibility, while high levels may encourage many birds to spend more time in the marginal vegetation. Early leafing-out of marginal and emergent vegetation will hide more birds from view than in a late season. The effect of these factors varies somewhat with the type of habitat and is more marked in regions of dense vegetation, particularly in the parklands and forests, where many of the water areas are bordered by trees.

4) Observers vary considerably in the number of birds they record in a given situation (Evans, 1956). Since most of the canvasbacks occurred in areas that were surveyed by only three crews, this can be an important factor. It may also be expected that fatigue will affect the percentage of birds recorded by any one observer.

5) In assigning unidentified ducks to species, it is assumed that the species composition of the unidentified birds is the same as of those that are identified. Since some birds are more visible under difficult conditions, or are more readily identified than others, this assumption is valid only within limits. Furthermore, many large groups of mixed species are recorded as "unidentified" owing to the impossibility of recording them with sufficient rapidity to separate them into species. It is probable that diving ducks (including canvasbacks), with their preference for larger waters, make up a high percentage of the population seen under such conditions. On the other hand, the canvasback, being a rather conspicuous bird, may very well make up a larger portion of the "identified" than is warranted by its actual occurrence.

6) Errors also may be caused by differences in methods. The speed and altitude of flight may vary with either the predilection of the crew or the type

of aircraft. Variations in terrain also will cause variations in speed and altitude, both increasing as the terrain becomes more rugged. A tandem-seating arrangement, with its attendant poor visibility for the rear-seat observer, may produce lower counts than a side-by-side arrangement. Furthermore, some crews fly at different times than others and the percentage of birds seen will be affected. In the Dakotas, during the years under study, the entire method of survey differed from the standard in that each important water area on the transect was circled by the aircraft until the highest possible count had been obtained. This resulted in a much higher than normal proportion of the birds present being recorded. In this paper, data from the Dakotas have been used as reported, with the result that canvasback population figures from these two states may be too high. However, the population segment from these areas is only 9 per cent of the total, so the total error from this cause probably is low.

Mapping of breeding-pair densities from individual 18-mile segments on the basis of one-year's data is subject to further difficulties, including very high sampling errors which cannot be evaluated. Furthermore, the fact that there is a great deal of variation in the percentage of the population identified under different conditions and by different crews leads to considerable bias error, since only birds directly identified as canvasbacks are used in the calculations. In view of these considerations, it seems very probable that data from 18-mile segments are a very unreliable measure of densities in their vicinity. Consequently, the lines delineating areas of different canvasback density may be imprecise.

The relationship between the density of breeding pairs and the eventual fall flight is another potential source of error. It is assumed in this paper that the fall flight is directly proportional to the breeding population. Therefore, the validity of using these data as weighting factors depends to a large extent on the degree to which the productivity of the adult population of birds is similar in all parts of the breeding range. This has not yet been determined.

There are many problems involved in using these survey data to determine summer distribution and to weight banded samples. If the survey were run primarily for these purposes, the sampling plan and the methods of operation would be modified. More emphasis also would be placed on the elimination and evaluation of bias errors. At present the breeding-ground survey furnishes the only numerical data available for these analyses.

The Winter Survey

The annual winter survey (January inventory) was first conducted in the United States in 1935, and since has been expanded to cover most of the wintering grounds in Canada, Mexico, Alaska, and the West Indies. The purpose of the survey is to determine the size and distribution of the waterfowl population in midwinter, but it is used also to some extent as a measure of the population remaining after the shooting season. For this paper, the winter-survey data provided information on the distribution of wintering canvasbacks and the volume of their migratory movements.

The survey in the United States is organized on a state basis by game management agents (law-enforcement personnel) of the Bureau of Sport Fisheries and Wildlife. A substantial part of the field work is carried out by personnel of the state conservation departments with bureau personnel participating. In Alaska, Mexico, and the West Indies, the surveys are both organized and conducted by technical personnel of the Bureau of Sport Fisheries and Wildlife. In Canada, the surveys are organized and conducted by the Canadian Wildlife Service, aided by provincial agencies. An attempt is made to cover all the parts of North America that are occupied by waterfowl at this season of the year.

For the purpose of gathering the data, each state or other survey area is divided into smaller areas. The degree to which these divisions are made is highly variable; in one state no subdivisions are made, while in Maryland the survey area is separated into 35 units.

In the winter inventory, the counts of most birds are visual estimates made from aircraft. The procedure varies greatly in intensity of coverage, timing of the survey, and equipment and personnel. The surveys usually are conducted throughout the day whenever weather is suitable for flying. Although the more important areas are covered by air, automobiles and boats also are widely used, particularly in areas of low waterfowl density. During the survey in January of 1956, more than 1,000 automobiles, 80 boats, and 150 aircraft were used.

Photography is sometimes used to advantage to obtain more accurate estimates of large concentrations of birds. Various grid systems occasionally are employed to help separate rafts of birds into units small enough to count.

The reliability of the winter-survey data depends on four major factors: (1) the accuracy of estimates of the numbers of each species; (2) the ability either to see all the birds of a species (regardless of their distribution), or to sample populations in such a way that the entire population can be estimated accurately; (3) co-ordination of effort so that birds are not missed or counted twice as a result of their movements during the survey; and (4) the degree to which total populations are accurately reflected by the survey units, so that the distribution of the population can be accurately known.

Little is known of the accuracy of visual estimates of large numbers of waterfowl. Spinner (1953)

found that visual estimates differed greatly even between trained observers. Because wintering canvasbacks occur in concentrated groups, only a few crews were responsible for almost the entire count used in the present study. Therefore, important errors could be caused by inaccuracies in visual estimates of waterfowl numbers.

The error associated with ability to see or properly sample the entire population at the time of the winter survey may not be as serious for canvasbacks as for some other species that are more widely distributed and less conspicuous. In coastal areas certain species occasionally are known to concentrate so far offshore that they are difficult to locate. While it is conceivable that canvasbacks might move out to sea, there is no evidence that they do.

In actual practice, co-ordination of the winter survey is difficult, since weather conditions may prevent aerial surveys for days at a time over much of the country. It is not unusual for the survey to require ten or more days in a single administrative flyway. Since the bad weather that causes delays in the survey also may cause movements of birds, considerable errors may result.

The extent to which the survey areas are divided into smaller units influences the reliability of the results when it is necessary to know the distribution of the birds within large areas. For example, the Virginia winter-survey data usually do not indicate where the birds were seen. Consequently, the exact distribution of waterfowl in the important lower Chesapeake Bay wintering area is unknown.

Although the degree of reliability cannot be determined for any portion of the winter-survey data, it is probable that errors occur. The canvasback is conspicuous because of its coloration and its habit of concentrating in large flocks on open water, so the greatest source of error probably is the visual estimation of numbers.

Band-recovery Data

Crissey (1955) discussed problems associated with the use of band-recovery data to indicate the comparative volume of movements over two or more migration routes. In our investigations, band-recovery data were used to indicate the course of migratory routes but were not used to indicate comparative volume (relative numbers of birds migrating along various routes). We have also used recoveries to obtain information on the distribution of the hunting kill in relation to breeding and wintering areas, the breeding-ground derivation of the hunting kill in various harvest areas, and the distribution of the total hunting kill. The reliability of information obtained from band-recovery data, as presented herein, depends on the extent to which the following are true:

1) The recoveries reported from a sample of banded birds truly reflect the characteristics of the population they are used to represent, i.e., the banded sample is representative.

2) The population from which a banded sample is taken is of known size and geographic distribution.

Each of these conditions will be discussed separately.

Representativeness of the band recoveries (Condition 1).—The extent to which reported band recoveries reflect the characteristics of a population depends upon the validity of three major assumptions.

A. The distribution of the kill of the banded sample is the same as the distribution of the kill of the population the sample represents.

There are many things to consider before one can be sure that this assumption is true. When the patterns of distribution of recoveries from birds banded in various parts of an area of reference are not the same, the banded sample must be properly distributed within it. The best way to insure proper sampling is to distribute the banding in a systematic or random manner within the population. Banding of canvasbacks on breeding grounds was done this way to some extent. Winter bandings, however, were concentrated at a few widely separated banding stations. Because of the unrepresentative distribution of the canvasbacks banded in winter, the recoveries of these birds could not be considered to reflect the characteristics of the entire continental canvasback population. If it were known that the distributional patterns of birds wintering over a wide area were essentially the same, then banding in one part of this area could be used to represent the entire area. For example, if canvasbacks wintering along the Gulf Coast of Texas had the same distribution as those banded in Louisiana, then the characteristics of the entire Louisiana and Texas Gulf Coast wintering population could be understood from the Louisiana sample. Lacking this information, the recoveries from winter bandings can be taken to represent only the population wintering in the immediate vicinity of the banding station.

If birds of various ages and sexes in a population could be banded in the correct relative numbers, recoveries of banded birds would be representative of the entire population. Unfortunately, many banding operations are selective for one age and/or possible sex. For example, canvasbacks banded in the summer were, to a very large extent, flightless young. Consequently, if the distribution of the kill had been based only on direct recoveries, this sample would indicate the distribution of the kill of the immature birds and not the entire population.

Another factor that may have influenced the representativeness of the banded samples analyzed for this paper was the need to combine data in order to have a large enough sample. In every instance, data from several years were combined. Comparisons sometimes were based on samples from birds of somewhat different spans of years. The estimates from the grouped banding data must be considered

to reflect average conditions. The likelihood that they reflect the situation in any specific year depends on the representativeness of the sample and the extent of the variability between years. At present there are insufficient data to appraise this.

In using band recoveries to indicate the course of migratory movements, it is assumed that the pattern of band recoveries is representative of the movement that occurred. Since hunting mortality is responsible for almost all recoveries, this assumption is true only to the extent that the hunting kill in an area is directly proportional to the number of birds passing through. Since the kill in an area depends on the hunting pressure and the length of time birds spend in the area, as well as the number of birds passing through, it is to be expected that band recoveries will not be evenly distributed along a population's migration route. Gaps in the pattern of recoveries, such as occur between the production and wintering areas of canvasbacks wintering on the Pacific Coast, complicate the interpretation of migration routes. Also, when the pattern of recoveries suggests a change in direction during migration, it is not known whether this change actually occurred or whether the apparent change in direction was a reflection of the pattern of shooting pressure. For example, the pattern of band recoveries indicated that a flight of canvasbacks left the major fall-migration route (between the Prairie Provinces and the Mid-Atlantic region) in Minnesota and Wisconsin and veered to the south down the Mississippi River. Although the pattern of recoveries suggested that this route probably was followed by a group of birds, there was still the possibility that the band of recoveries down the Mississippi River Valley simply meant that birds were harvested there from migration routes that crossed rather than followed the river.

B. The proportion of recovered bands that is reported is the same for all areas at all times.

In the analysis of banding data in this paper, it was assumed not only that the banded sample was representative of a population, but also that the reported band recoveries were representative of all band recoveries whether reported or not. If the proportion of recovered bands that is reported is higher in some areas or at some times, the data will be biased. There are at least two reasons why the proportion of reported bands may vary: (1) Hunters in some areas may be more inclined to report bands (although it is not known whether or not this is true). (2) Efforts of conservation agencies to collect bands at checking stations or during bag checks may vary from area to area or year to year (as is known to occur). The importance of the variations in band-reporting was not evaluated. However, this bias may be less serious for the canvasback than for other species because relatively few canvasbacks pass through checking stations.

C. The banding samples are large enough to minimize the importance of sampling error.

This assumption is not fully justified, for relatively small numbers of canvasbacks were banded. Therefore, relatively few recoveries were available for certain calculations. For example, the distribution of the kill of birds banded on various breeding grounds was determined on the basis of the following numbers of recoveries: southern Manitoba, 188; southern Saskatchewan, 135; British Columbia, 45; North Dakota, 44; South Dakota, 26; Alaska–Yukon, 25; southern Alberta, 21; and Lake Claire–Athabaska delta, 16. Since the number banded is not known, the sampling error cannot be estimated precisely. However, judging from the number of recoveries in the smaller samples, the error in the estimated kill for certain harvest areas could equal or exceed 100 per cent at the 0.05 probability level. Even for Saskatchewan, the most important production area, a sampling error of roughly ± 70 per cent (probability 0.05) could occur. It must be concluded that the distribution of recoveries from any given production area to any specific harvest area may be considerably in error owing to chance. It is obvious that it would be very desirable to have larger samples.

Sampling error of the estimate of total kill within a harvest area should be smaller because this estimate usually is based on contributions from several production areas. For example, if it is assumed that a sample of 1,500 banded birds contributed information on the canvasback kill in the Mid-Atlantic region, the sampling error would be about ± 20 per cent at the 0.05 probability level.

Although the confidence limits around estimates based on the meager data used in this study are wide, it should not be assumed that the estimates actually are in error to the degree the confidence limits suggest. If an infinite number of estimates were based on samples from the same population, only 5 per cent would depart from the true mean as much as the estimated confidence limits. In most instances the sample data will be more accurate. It should be recognized, nevertheless, that sampling error can be important when the number of recoveries is so small.

Definition of populations that band recoveries represent (Condition 2).—In order to analyze correctly data based on samples, it is essential to understand the population being sampled. For this paper it was essential to know the relative size of populations sampled by summer banding. This was necessary because the numbers of birds banded in each population were not in proportion to the size of the population. Consequently, in order to obtain information concerning the entire continental population, the band-recovery data had to be given their proper weight. The extent to which band recoveries were properly weighted depends both upon the reliability of aerial breeding-population surveys and

upon the validity of the assumption that the size of the fall flight from a given production area is directly proportional to the size of the breeding population. The breeding-ground survey and its limitations already have been discussed.

All populations probably are not subjected to the same shooting pressure. This factor should be considered when band-recovery data are used to estimate the size and breeding-ground derivation of the hunting kill in various harvest areas. The band-recovery data should be adjusted so that the recoveries representing heavily shot populations receive more weight than those representing lightly harvested populations. Unfortunately, information concerning the size of some of the banded samples used in this study was not available. Consequently, differences in recovery rate could not be determined. Therefore, it was necessary to assume that these differences were not great, and that the hunting kill of each breeding population was almost directly proportional to the size of the canvasback population.

The reliability of a weighting factor also depends upon how accurately the limits are known for the population represented by the sample. For example, it was assumed that the sample of canvasbacks banded in southern Saskatchewan was representative of the entire fall flight from southern Saskatchewan. Therefore, the recoveries from these bandings were weighted by the breeding-pair index value obtained for all of southern Saskatchewan. If, in fact, the banded birds represented a population of a different size, then this weighting factor was incorrect. The probability of this sort of error occurring would be much less if birds from all parts of an area had essentially similar distribution patterns. However, Figs. 4, 5, and 6 clearly indicate that birds in different parts of a province or state have different distribution patterns. Consequently, unless the banded samples are properly allocated (which is unlikely), errors will result.

The reliability of information obtained from the analysis of band-recovery data depends very heavily on the reliability of the weighting factors. For this reason, the results of the present study should be reinterpreted when better information becomes available concerning the size of the fall flight from production areas.

Hunter-kill Mail Survey

The Bureau of Sport Fisheries and Wildlife has conducted a mail survey of waterfowl hunters each year since the 1952–53 hunting season. The objective of this survey is to estimate the total kill of ducks (all species combined) for each administrative flyway with a sampling error not to exceed 5 per cent. For the present paper, the kill-survey data were used to estimate the kill of one species, the canvasback, in single states or groups of states. The survey is conducted as follows: Names and addresses of a sample of hunters are obtained through the co-operation of the Post Office Department at the time federal migratory bird hunting stamps are purchased. These hunters are contacted at post offices selected at random in each state. The number of hunters contacted in each state is proportional to the sales of migratory bird hunting stamps in that state. Questionnaires are sent each year to a total of about 35,000 hunters, of which about 24,000 eventually respond.

Investigations conducted on four study areas indicated that the waterfowl hunting kill reported by hunters was greatly exaggerated and procedures were developed to correct this error. This was discussed in detail by Atwood (1956). The same studies also revealed bias errors in the species composition of the reported kill, and corrective measures were developed. Since the canvasback was taken on the study areas only rarely, the effectiveness of the corrections of the reported canvasback kill is unknown. Because of the original objectives of the survey, i.e., estimates of the total duck kill on a flyway basis, and owing also to the complex sample design necessary because post offices were used as sampling units, the sampling error for a particular species on a specific area is unknown at present. This subject is being investigated currently. In using data from this survey to obtain the information presented in this paper, it is assumed that either the procedures used to remove bias errors do properly correct the reported canvasback kill for each flyway, or else the procedures alter the reported flyway totals to the extent that the bias is the same in all flyways. It is assumed also that the bias errors in the canvasback kill reported from each state in a flyway are the same. The extent to which these conditions are satisfied is at present unknown. However, results concerning the distribution of the kill that were obtained by this procedure agreed well with those based on weighted band recoveries.

Consistency of Canvasback Data from Various Sources

The reliability of much of the data used to prepare this report is unknown, and some of it is impossible to evaluate. In order to determine if population and kill data were consistent when viewed as a whole, the following data can be compared:

Average breeding-population index (1953–56)	363,100
Average winter-inventory count (1952–56)	508,000
Average annual hunting kill in the United States based on the hunter-kill survey (1954–56)	339,838
Average total annual hunting kill based on hunter-kill survey and band recoveries outside of the United States (25 per cent of total kill outside of U.S.)	526,102

The breeding-population survey and winter-inventory count should represent essentially the same population, provided relatively little mortality occurs between January and May. The breeding-population index should be less than the true population to the extent that breeding canvasbacks are not seen from the air. Air–ground comparisons suggest that roughly half the canvasbacks are seen. However, the manner in which data from unidentified ducks are handled in adjustments of the aerial-survey data probably increases the canvasback count. Thus, it seems reasonable that the aerial breeding-population count is 71 per cent of the winter-inventory count. Both the breeding-ground survey and the winter survey suggest that the average annual breeding population during 1952–56 was about 500,000.

The next problem is the reasonableness of the estimated kill figure. This is difficult to evaluate when information on productivity and/or total annual rates of mortality is not available. However, if it is assumed that 40 per cent of the adult canvasbacks are females, that 80 per cent of the females succeed in raising broods, that the average brood size at flying age is 4, and that there is a 10 per cent adult mortality between May and September, then a fall flight estimate of 1,090,000 can be made. The total estimated bag of 526,102 implies a kill of 48 per cent of the fall flight, and leaves about 564,000 canvasbacks. A crippling loss and nonhunting loss of an additional 64,000 or an additional 6 per cent is not unreasonable. This would reduce the winter population to the 500,000 level suggested by the winter-inventory and breeding-population surveys. Thus, it appears that the procedures used to obtain breeding-population counts, winter-inventory counts, and estimates of the total hunting kill yielded estimates of reasonable magnitude.

Although the average breeding and wintering population counts are of reasonable magnitude, they probably are not of sufficient accuracy to measure any changes in population density that may have occurred during the period 1953–56. In all possible comparisons, the two surveys trended in opposite directions. Apparently one or both of the surveys is not precise enough to correctly measure annual population changes of the magnitude that occurred during 1953–56. This, of course, assumes that mortality between the winter and breeding-ground surveys is either constant or insignificant.

Another test of the consistency of the data can be made by considering together Fig. 14 (diagrammatic map of migratory movements), Fig. 15 (estimated distribution of the hunting kill), and Fig. 3 (distribution on the wintering range). These figures show that the population wintering in the eastern United States is about nine times as large as the population wintering on the Pacific Coast. Despite this large estimated difference in the number of birds, the hunting kill of the eastern population is only 2½ times greater than the west-coast kill. This suggests that the west-coast birds sustained a heavier shooting pressure than the eastern population. However, some of the discrepancy probably is the result of either a biased distribution of band recoveries, inaccurate winter-inventory figures, or band-recovery weighting factors that are in error.

REFERENCES CITED

ALDRICH, JOHN W., ET AL. 1949. Migration of some North American waterfowl. U.S. Fish and Wildl. Serv., Spec. Sci. Rept. (Wildl.) No. 1:1–48.

ATWOOD, EARL L. 1956. Validity of mail survey data on bagged waterfowl. J. Wildl. Mgmt., 20(1):1–16.

CARPENTER, J. RICHARD. 1940. The grassland biome. Ecol. Monog., 10(4):617–684.

COCHRAN, WILLIAM G. 1953. Sampling techniques. New York:Wiley & Sons. 330pp.

CRISSEY, WALTER F. 1955. The use of banding data in determining waterfowl migration and distribution. J. Wildl. Mgmt., 19(1):75–84.

———. 1957. Forecasting waterfowl harvest by flyways. Trans. N. Amer. Wildl. Conf., 22: 256–268.

EVANS, CHARLES D. 1956. Progress report/ Breeding ground surveys in Quebec and Labrador. Unpubl. report, filed Bureau Sport Fisheries and Wildlife, Wash., D.C. 17pp.

FENNEMAN, NEVIN M. 1931. Physiography of western United States. New York:McGraw-Hill. 534pp.

———. 1938. Physiography of eastern United States. New York: McGraw-Hill. 714pp.

HOCHBAUM, H. ALBERT. 1944. The canvasback on a prairie marsh. Washington, D.C.:American Wildlife Institute. 201pp.

PUTNAM, DONALD F., BENOIT BROUILLETTE, DONALD P. KERR, AND J. LEWIS ROBINSON. 1952. Canadian regions. New York:Thomas Y. Crowell Co. 601pp.

SMITH, ALLEN G. 1956. Progress report/ The 1956 aerial and ground waterfowl surveys in Alberta, Canada. Unpubl. report, filed Bureau Sport Fisheries and Wildlife, Wash., D.C. 34pp.

———. 1957. Part II. A progress report/ On the aerial surveys of the Vermilion waterfowl study area 1953–1956 Vermilion, Alberta, Canada. Unpubl. report, filed Bureau Sport Fisheries and Wildlife, Wash., D.C. 20pp.

SMITH, J. DONALD. 1946. The canvas-back in Minnesota. Auk, 63(1):73–81.

SPINNER, G. P. 1953. Efficiency of the photographic guide method in increasing accuracy in estimating numbers of waterfowl. 9th Proc. N.E. Sect. Wildl. Soc. 8pp+2 tabs. Mimeo., filed Patuxent Research Refuge, Laurel, Md.

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MOVEMENTS, DENSITY, AND MORTALITY IN A BLACK-TAILED JACK RABBIT POPULATION

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The black-tailed jack rabbit (*Lepus californicus*) occurs in the western United States from Iowa to the Pacific Coast and southward into northern Mexico. Throughout its range it is important to man either as a crop depredator, a game animal, or a carrier of disease. It is the purpose of this paper to present certain data on home range, movements, density, and mortality of a population of this hare in the Sacramento Valley, California, with the hope that they will add to our knowledge of the ecology of this species.

Funds and equipment for the study were provided by the Museum of Vertebrate Zoology and the Zoology Department of the University of California, Berkeley. John B. Cowan and other personnel of the Gray Lodge Waterfowl Management Area contributed their time, efforts, and facilities. A. S. Leopold, O. P. Pearson, W. C. Reeves, and R. D. Taber added many helpful suggestions. To these persons and to others who helped in any way, I extend my sincere thanks.

Study Area

A population of the black-tailed jack rabbit was intensively studied from October 1954 to March 1956 on the Gray Lodge Waterfowl Management Area, Butte County, California. This area embraces about 6,800 acres managed primarily for waterfowl by the California Department of Fish and Game. Over 2,000 acres consist of ponds and marshes, and much of the remainder is planted to crops such as rice, millet, barley, and milo. There are many miles of irrigation ditches and dirt roads. Some fields are left fallow; these, as well as the ditch banks and roadsides are grown to an assortment of weeds, many of which are beneficial to wildlife. The surrounding farms are similar to the management area but are less weedy and have a lower ratio of edge to fields. The soil on the area is an adobe-alkali type. Most of the rain falls from October through March. Winters are mild, with the temperatures seldom below freezing, and summers are hot with temperatures often exceeding 100°F.

Methods

Two methods were used to study the jack rabbits. One method consisted of the examination of a sample of 485 jack rabbits killed over the 18-month period. Each hare was examined for its general physiological condition and the presence of any gross lesions and internal or external parasites.

The second method consisted of capturing a series of the jack rabbits alive, marking, releasing, and observing them. The hares were captured in individual traps about 3 feet long and 1½ feet high, with a sliding door at each end. Fig. 1 shows one of these traps with a captured jack rabbit. The hares were enticed into the traps with apples.

The hares were marked with two plastic discs in one ear and a tattooed number in the other ear. The discs were held in place with a tiny metal rivet and washer (Tyndale-Biscoe, 1953). Symbols were painted and engraved on the discs, and some of them were coated with glow beads to facilitate night observations.

Three separate sites within the management area were selected for trapping. The hares were marked with yellow, red, or blue discs, depending on the area where they were captured. The three trapping areas are referred to in the present paper as the yellow, red, or blue area, according to the disc color used. This system was de-

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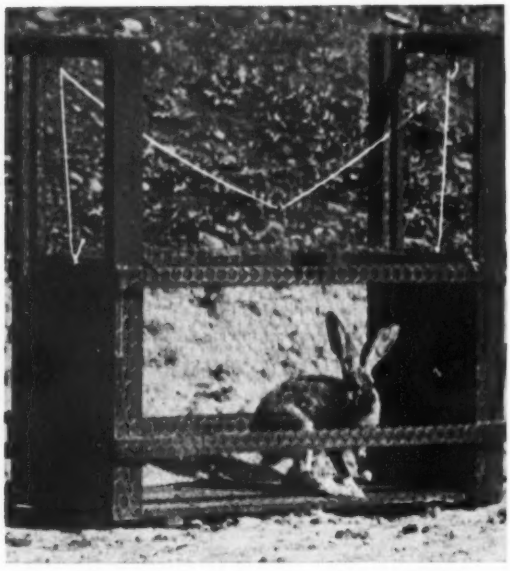

FIG. 1. Trap with a captured jack rabbit.

signed to provide a maximum of information regarding extensive movements, for it could not be hoped that the disc symbol could be read each time a marked hare was observed.

The hares were observed with 6× binoculars and a 20× telescope. Observations were made in the morning and evening by hiding in some convenient location and watching the animals on their feeding excursions. At other times, walks were taken through the fields or along the roads, and the hares were observed as they were flushed from their forms.

LIVE-TRAPPING RESULTS

A total of 677 trap nights resulted in the capture of 143 jack rabbits. Thirty-five of the captures were recaptures of 17 individuals. The majority of the recaptures were single occurrences, but several were double, and one hare was caught six times in ten days. In general, the hares were not readily retaken, even though observations indicated that they remained for long periods in the vicinity of the traps.

A total of 100 jack rabbits (56 males and 44 females) was marked and released. There were no sight records for 25 of these marked hares, but three of these 25 were recaptured within a few days and two were found dead, leaving 20 marked animals that could not be accounted for. Both of the dead hares were found soon after they died, one 18 days after its release and about 200 yards from its release site, and the other about 2 months after its release and about ½ mile from its release site. Eleven of the hares that were never accounted for were trapped early in the study when visits to the area were not too frequent; thus, there was sufficient time for them to have disappeared from the population.

Numerous observations were made on the other 75 hares. Twice as many observations were made per male as per female. This disparity between the sexes seems to be associated with increased activity of the males during the breeding season, for at this time of the year the number of observations per male rose sharply, whereas the number per female remained at approximately the pre-breeding season level.

HOME RANGE AND MOVEMENTS

Home range, as used in this paper, follows the generally accepted concept given by Burt (1943), who defines it as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young." Occasional sallies outside of the area are generally excluded from the home range proper.

My observations indicated that the jack rabbits tended to remain within rather well-defined areas of less than 50 acres, even in larger fields where no distinct physical barriers to greater movement occurred.

Figs. 2 and 3 show the ranges of several hares within field No. 23 (red area). This field was an excellent feeding place for jack rabbits and an area where they could easily be observed. In December 1955 and January 1956, rain fell almost every day, and the entire west end of the management area, including field No. 23, became covered with water (Fig. 4). Although the fields were flooded, most of the roads and higher levees remained above water. During this time the hares were forced to move from the fields and seek shelter along the surrounding roads

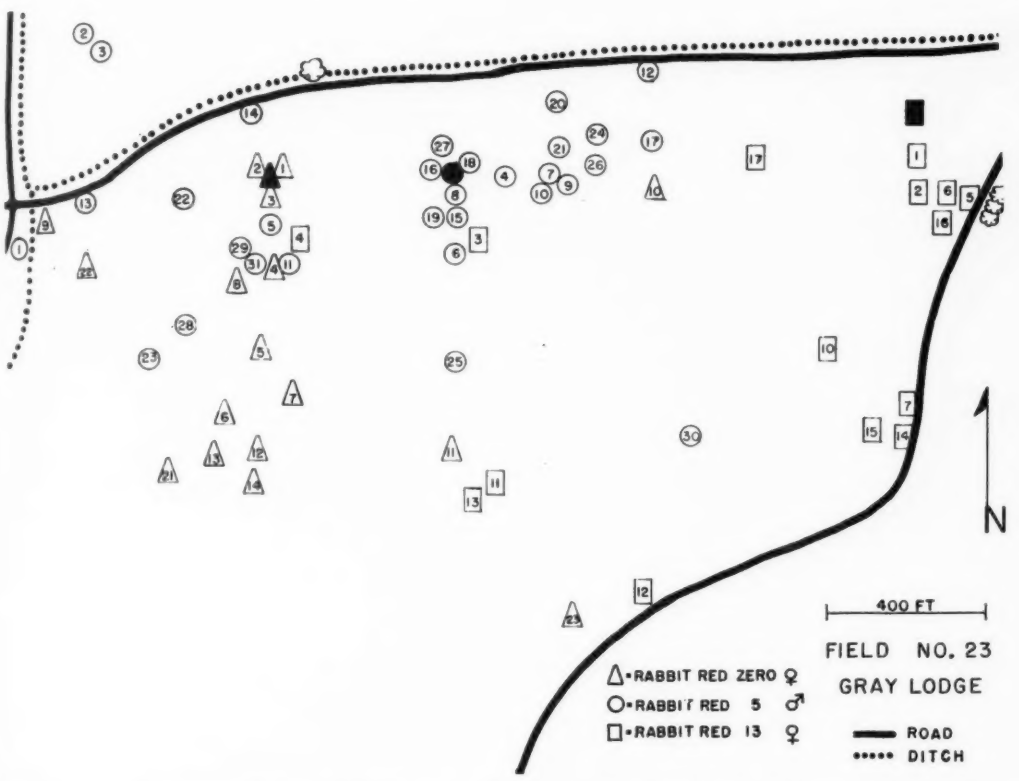

FIG. 2. Known ranges of three different jack rabbits in field No. 23. Numbers refer to successive observations. Solid symbols indicate the site of original capture.

and levees or travel to unflooded fields to the north and east. This period of the study is hereafter referred to as the "flood."

Prior to the flood, 44 hares had been marked and released in field No. 23. During November and early December, 33 (18 males and 15 females) of these were known to be living in and about the field. In January and February, during the flood, 26 (13 males and 13 females) of these 33 were observed at various places elsewhere on the refuge (Fig. 4). Eight were found over a mile from the sites where they were first captured, and the remainder were located along the roads surrounding field No. 23. Seven of those that moved to distant areas were females, and only one was a male. This may indicate that males have a stronger tendency to remain within their home ranges during times of stress. Three (*A*, *U*, and *R*) of the 26 that were located were found dead along the roads bordering field No. 23 and one (*Circle E*) was shot while I was making a collection of hares in late February. Of the original 33, this left 29 that may or may not have been alive at the end of the flood. After the water receded, 12 of these 29 returned to field No. 23, including one (*J*) that had not been located during the flood period, and three of the eight that had traveled to unflooded areas. All three of those returning from long distances (over ½ mile) were females.

Intensive searches of the entire study area near the end of the study revealed only three of the 29 to be still alive and not returned to field No. 23. Of these three, two (*Y* and *V*) were seen along the north road of field No. 15 not far from their former ranges. One (*Circle C*) was seen near the northwest border of field No. 17 about 1 mile from the place where it was first cap-

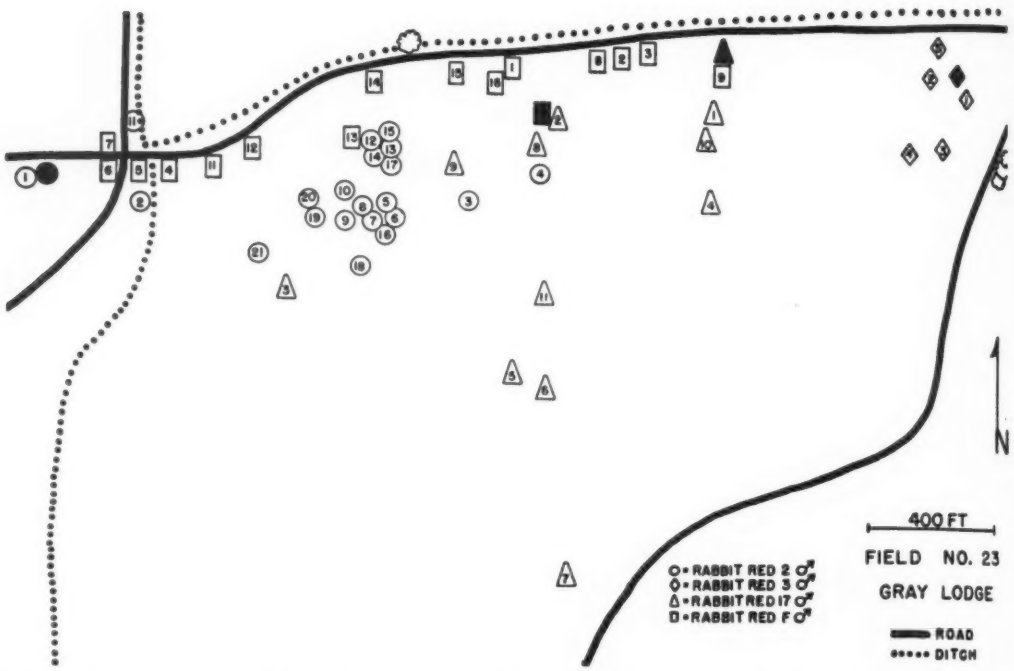

FIG. 3. Known ranges of four different jack rabbits in field No. 23. Numbers refer to successive observations. Solid symbols indicate the site of original capture.

tured. Evidently it remained in this area, and its carcass was found here in the late summer of 1956.

Figs. 2 and 3 illustrate certain aspects of the home ranges of the hares in this population.

Red Zero (Fig. 2), a female, was first captured February 3, 1955, and was still alive at the termination of the study on March 25, 1956. During these 14 months, it was seen or recaptured on 23 different dates. All of these observations, except during the flood, were within the western half of field No. 23, in an area of about 50 acres. During the flood, this female was observed on five different dates within a 25-acre area of field No. 17 about 1½ miles distant (Fig. 4). Searches of field No. 17 failed to reveal it during the first week of March, and on March 19 it was seen back in field No. 23 almost in the center of what I considered to be its former range. Here it remained until my study was terminated.

Red 13 (Fig. 2), another female, was first trapped on May 22, 1955, at the opposite end of field No. 23 from *Red Zero*. All of the observations made on it within this field were more or less concentrated at the east end of the field. During the flood, it was observed several times in field No. 24 about 1 mile distant (Fig. 4), and it, too, returned to field No. 23 when the water receded, and again to the same general area of the field where it formerly ranged.

Red 5 (Fig. 2), a male, was captured on February 19, 1955, and was subsequently observed 31 times in and about field No. 23. During the flood it did not travel far and was seen several times along the north boundary road of field No. 23 within what was considered to be its former normal cruising area. As soon as the water receded, it returned to the field and remained within its previously known range until it was shot at the end of the study.

By comparing the known ranges of the three hares shown in Fig. 2 with those shown in Fig. 3, it can readily be seen that there is considerable overlap between the ranges of individuals. It is also evident

that there are certain patterns of home ranges within the field. Thus, *Red 5* (Fig. 2) and *Red F* (Fig. 3) have ranges of about 40 acres, the general outlines of which are oblong and follow along the north border road. *Red Zero* (Fig. 2) and *Red 17* (Fig. 3) have ranges that extend out into the field rather than along the road. *Red 13* (Fig. 2) has a range that parallels the east border road. Each of these ranges is less than 50 acres in extent and includes the site of original capture of the hare. *Red 3* (Fig. 3), on the other hand, seems to have shifted its range from the unnumbered field west of No. 23 where it was originally captured, settling down in a more or less ellipsoid area of about 50 acres in the northwest end of field No. 23.

None of the hares used the entire field during their normal travels; however, when flushed, they frequently traveled the length of the field, only to circle back and return to the areas from which they were flushed. Sometimes the hares would be back near the area from which they were chased even before I had left the field, and, if left undisturbed for only a few minutes, they resumed their former activity of feeding or resting.

There appears to be a tendency for jack rabbits to return to or near their former ranges, even when they are driven from them for either a short period or for considerable lengths of time (over 1 month). They seem to possess, as shown by those that returned after the flood, a facility for finding formerly occupied areas even when they have traveled over 1 mile from them. The mechanisms involved in this "homing" are not known, but in this study all of the

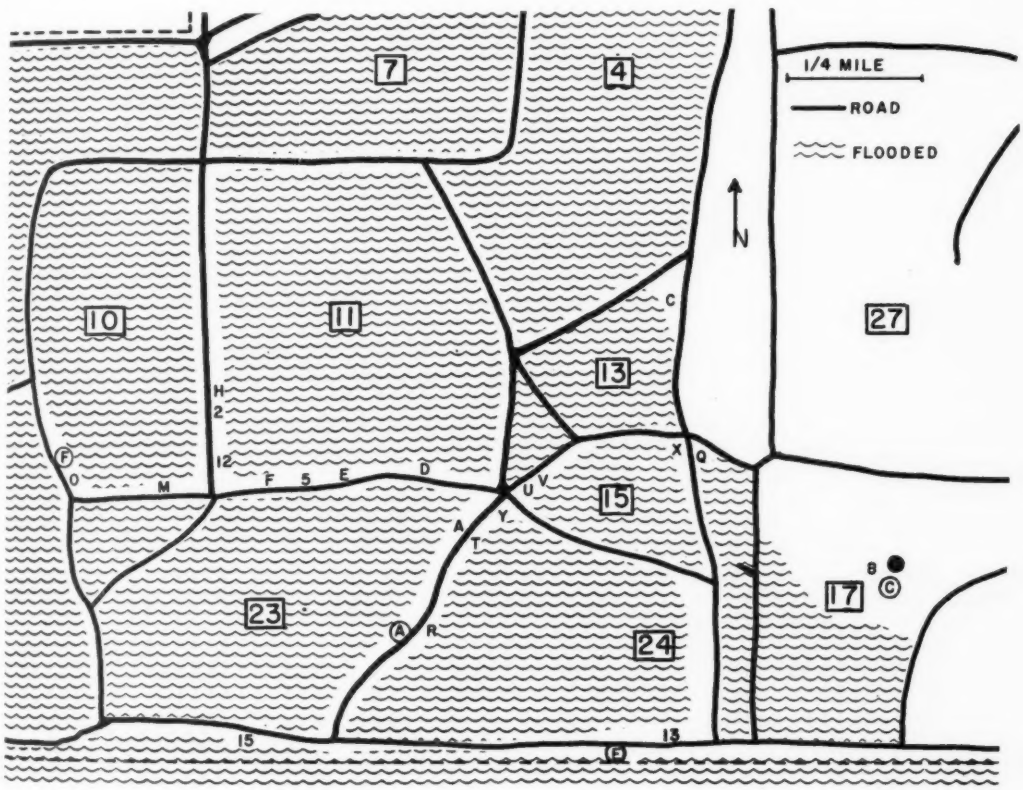

FIG. 4. Known locations of marked jack rabbits from field No. 23 during the winter flood of 1955–56. Numbers in squares are field numbers. Plain numbers and letters and circled letters refer to symbols on the ear discs of the jack rabbits. The solid circle is jack rabbit *Red Zero*.

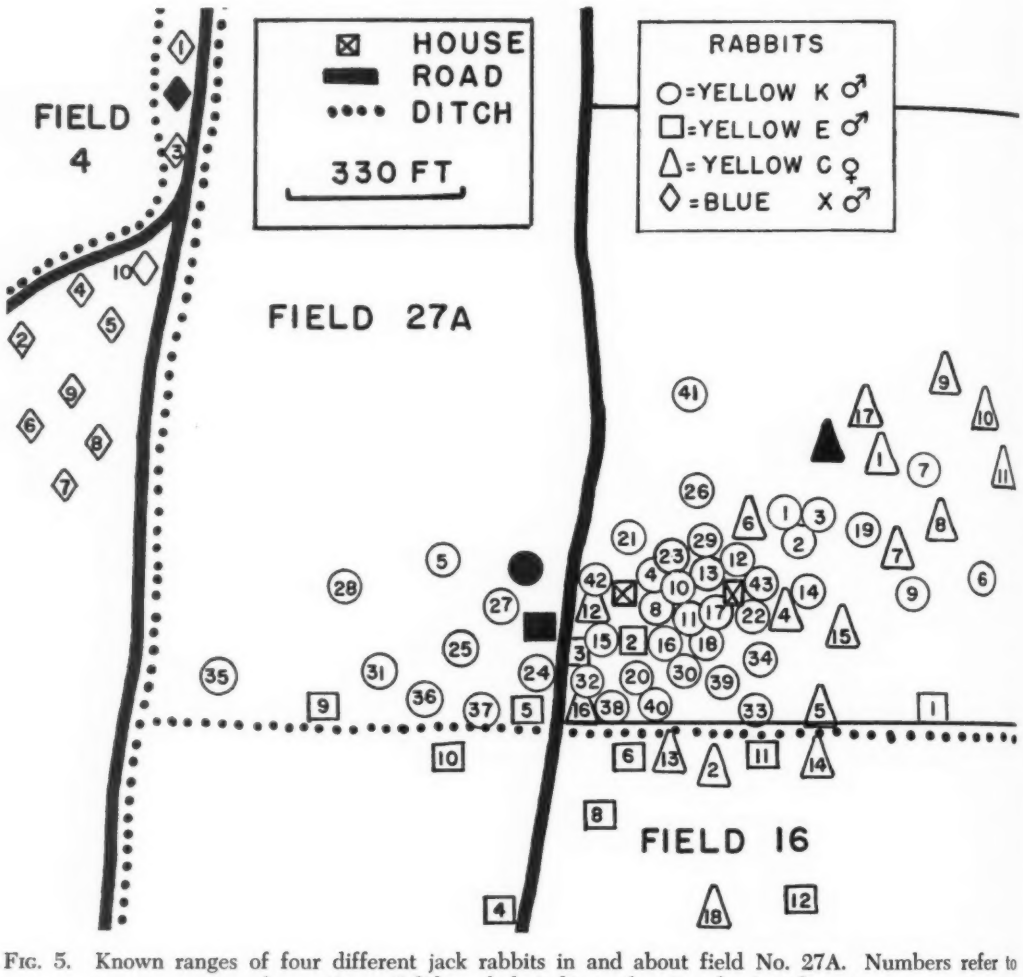

FIG. 5. Known ranges of four different jack rabbits in and about field No. 27A. Numbers refer to successive observations. Solid symbols indicate the site of original capture.

returns can probably be explained on the basis of random wandering. *Red Zero*, for example, apparently left field No. 17 where it had gone during the flood, at least two weeks before it was seen back in field No. 23. It was not observed during this intervening period, even though intensive searches were made of fields Nos. 17 and 23. It can be assumed that it was wandering during this period, perhaps pushed on by some urge to find the area where it formerly lived.

Fig. 5 shows the known ranges of three of the yellow-area animals and one of the blue-area animals. Field No. 27A and the surrounding areas were not flooded during the winter flood period. Field No. 27A was plowed and planted to barley in the fall of 1954, but mostly weeds and isolated patches of barley came up. In September 1955, a portion of the weeds in the west end of the field was burned, leaving a clear area that produced green grasses and forbs. The areas to the north and east of this field were flooded for use as duck ponds from October 1955 to February 1956. Field No. 16 was planted with millet in the fall of 1955, and the water was left standing on it until February 1956. In the yellow area, therefore, there existed an ever-changing pattern of land available for the hares, shrinking in the late summer and fall when the hare population was high, and enlarging in the early

spring when the population was low. Thus, in the winter, the hares were crowded into a much smaller area than in the summer. This was the general pattern of availability of habitat throughout the study area.

The data presented in Fig. 5 support the conclusion drawn from field No. 23, that the hares have rather well-defined home ranges that do not extend over the entire area of the field available to them. The hares in this field had ranges of about 30 to 35 acres, whereas those in field No. 23 had ranges slightly larger, averaging perhaps 45 acres. This difference may be due to the fact that there are more barriers, such as levees, fences, and ditches in field No. 27 than in the open expanse of field No. 23. These obstacles seem to have a definite effect on the normal travels of the hares, but present little or no barrier to movements when the animals are alarmed.

From observations made on the hares in and about field No. 27, it became evident that an animal may use all of its known range in a very short period of time, even under what appear to be quite ordinary circumstances. Thus, animal *Yellow K* (Fig. 5), which was marked on October 11, 1955, and observed on 39 different days up until the end of the study, was known to travel during this time over an area of about 25 to 30 acres, but on several occasions it was seen to cover this same area in the short interval of an hour. The range of this hare is probably the best known of any in this study, for the animal was seen within this range during every month at almost every time of day. It was seen feeding, drinking, resting, playing, and carrying on sexual activities all within the confines of this range.

It appears from the data in this study that female jack rabbits may have home ranges that are larger than those of males. For example, *Yellow C*, a female, appears to have a larger home range than either *Yellow K* or *Yellow E*, both males (Fig. 5). Other instances of females with apparently larger home ranges than the males were found in both the red and blue areas. The greatest movements recorded in any area were those made by females.

The observations on *Yellow C* and *Yellow E* that place them in the central part of field No. 16 (Fig. 5, squares 8 and 12; triangle 18) were made during February and March 1956, after the water had been removed from the millet. At this time green grasses and forbs began to sprout, and field No. 16 became an excellent feeding area. The hares were quick to take advantage of the feed and within a few weeks as many as a dozen of them could be seen within the field on evening feeding excursions. This pattern of shifting into previously flooded areas when the water was removed was repeated all around field No. 27A. It appears that there are shifts in the home range that may involve either an enlargement of an already existing range, or an entire shift of range with abandonment of all or part of the former area. My data on the latter phenomenon are few, because these shifts of ranges appear to require a considerable period of time and the study had to be terminated just when such shifts were occurring.

Blue X (Fig. 5) was captured along the road to the east of field No. 4. During the flood this area was under water, and the hare was forced to leave. It moved only slightly south, to field No. 13, and set up what appeared to be a new range, even though this field was already occupied by other hares. Here it remained until the study was concluded. This movement may be interpreted in two ways: either as an enlargement of a previous range from the border of field No. 4 into field No. 13, or a reduction of a previous range that included both the border of field No. 4 and field No. 13. *Blue O* and *Blue S*, on the other hand, moved from the border of field No. 4 across the road and deep ditch to the west of field No. 27 and into field No. 27A. They were observed in the latter field for several months prior to the end of the study. It appears that they had successfully shifted their ranges from one field to another.

Shifting, expansion, and contraction of the home range undoubtedly are factors that allow for the quick population of fields that had formerly not been suitable for

occupation. The data from marked hares strongly suggest that the movements into areas that have been removed as suitable habitat for only a few months may involve some animals that formerly ranged there.

Although only a few observations were made at night, the greatest movements of hares in this study were detected at this time. It may be that during the night they move farther than one would suspect from observing them during the day, evening, or early morning. In field No. 27A the hares were seen converging on the more open west end of the field as evenings approached. In the mornings their movements were reversed and they were seen to go from the open area into the more weedy portion to rest for the day. It is possible that during the night they wander even farther, going to places where they are never seen during the day.

The home ranges of the jack rabbits, as determined in this study, seem to be rather small, averaging perhaps 45 acres. Undoubtedly, the size of the home range is affected by the pattern of the environment. Thus, on Gray Lodge Waterfowl Management Area, where food, water, and cover are found in close proximity, jack rabbits need not range far. On the Santa Rita Range in Arizona, jack rabbits were estimated to have home ranges several miles in diameter, and daily movements of 1 to 2 miles from food to shelter were common (Vorhies and Taylor, 1933). Orr (1940) reports several instances of jack rabbits feeding at distances up to 1 mile from suitable cover.

NUMBER OF JACK RABBITS ON THE AREA

Several methods of census were tried to determine the number of jack rabbits on the study area. It was obvious that one person, in the short time available, could not census the whole area directly. Therefore, efforts were concentrated on fields Nos. 23 and 27, where marked animals were available.

Strip counts, based on the method of Webb (1942), were attempted in field No. 23. It became evident that such counts were not reliable because of the extreme variation in flushing distances. Some of the hares were active when the field was entered, some flushed at ranges up to 100 yards, and others flushed only when approached to within a few feet. With the high densities encountered, there were often as many as 20 hares running ahead of me on these counts. As the running hares passed others that were resting, there seemed to be a spread of the alarm, and the resting hares flushed long before I was near. Although these counts were not successful in the late fall, I feel that they may be of use in censusing jack rabbits on a warm, clear day in late summer (August to September) between the hours of 11 A.M. and 3 P.M. At this time of the year and day, jack rabbits are most likely to be inactive and to respond in a similar manner.

Counts were made of the hares as they were seen feeding in early morning or late evening. Such counts always yielded population figures that were much lower than other estimates. Furthermore, they varied greatly from day to day and at different times of the year. On cloudy, cool days the evening feeding counts were consistently higher than those on hot, clear days. Counts at different times of the year were greatly affected by the changing patterns of vegetation.

The rather open, flat expanse of field No. 23, bordered by levees, allowed another type of count to be made. This I term a "total count" for want of a better name. The field was entered at midday from the northwest corner. A strip closely paralleling the west levee was then walked in a southerly direction. While I was walking this strip, I made an estimate of the minimum flushing distance on either side of the strip. This distance was then used as the width between subsequent north and south strips, and the entire field was covered in this manner. To eliminate counting the same animals twice, only those that ran to the west or that crossed the levees were counted. The hares tended to travel in a circle, crossing back toward the places where they had been flushed, but some left the field. When this method was used, the 20× telescope mounted on a

rifle stock was an indispensable tool for checking the far ends of the field. Counts made in this manner were used as an index of the minimum number of hares present in the field at any date.

Sometimes when I was observing the hares, counts were made of the number of marked and unmarked animals seen. These figures were then used to estimate the total population by means of the Lincoln Index (Leopold, 1933). The accuracy of the estimate made with this method is seriously affected by mortality of marked animals between the time of marking and the time of observation. To eliminate this bias, the number of marked hares known to be alive on the observation date, rather than the total number previously marked, was used as the total number of marked animals in the field on that date. Thus, it was possible to use this method only when and where very intensive observations were being made and all living marked animals could be accounted for. Although this method has its own bias, I feel that it provides a more reasonable estimate than would be obtained if the mortality were entirely ignored.

The Lincoln Index system indicated that approximately 162 hares were using field No. 23 during the months of November and December 1955. Most of the counts used to calculate the total population were made during evening feeding periods of the hares. Since it was known that the ranges of some of the marked hares feeding in field No. 23 extended outside it, an area to take this into account was added to the field area to determine the total census area. From observations on marked hares, it seemed that the addition of about 30 acres would be sufficient. The total area censused was accordingly estimated to be approximately 160 acres, rather than the 130 acres within the field itself. The density of the hares in field No. 23 during the fall of 1955 was then approximately one hare per acre. Total counts during this period gave estimates of approximately 100 hares within the field itself (approximately 0.8 hare per acre), and the highest feeding count recorded during this period was 80 hares.

During the flood, there were no jack rabbits in field No. 23, but as soon as the water receded, they returned to it. By early March, the field was almost as dry as it had been in the fall, and counts were resumed. During March, 12 marked hares were known to be again using the field, and the ratio of marked to unmarked hares seen at several feeding observations indicated a total population of approximately 73 hares. Total counts made in this month indicated a population of about 55 hares and the highest feeding count was 31 hares.

On a drive-shoot conducted in field No. 23 on March 23, 1956, 46 hares were killed, including seven of the 12 marked animals considered to be available. The observers stationed along the levees during the drive-shoot reported 17 hares that escaped the drive. Thus, a minimum of 63 hares was known to be in the field at that date. The ratio of marked to unmarked hares shot gives an estimate of 79 hares in the field.

In the yellow area, during November and December 1955, the Lincoln Index method gave a figure of 103 hares. Much of the area at that time was artificially flooded for use as duck ponds, and it was estimated that approximately 90 acres were being censused. This, then, gives a fall population of approximately 1.2 hares per acre. During the winter flood, this area was not seriously affected. Estimates by the same method placed the number of hares in the area in January 1956 at 109, and by February and March it rose to 132. Thus, the population here increased by influx during this period. The presence of blue-area hares in the yellow area was further evidence of this influx.

In order to arrive at a population figure for the entire live-trapping area, it was necessary to determine if the hare density in fields Nos. 23 and 27 was indicative of the density over the remainder of the study area. Eight roadside counts of hares were made at various times by driving slowly along all of the roads of the management area west of field No. 27. Each of these counts was made from about 1½ hours before dark until it became too dark to see. As one would

suspect, these counts varied greatly, depending upon the weather, the behavior of the hares, and the pattern of vegetation. The total number of hares seen on all counts was 804, and of this total 88 (11 per cent) were seen within field No. 23. By subtracting the pond areas from the total area covered, it was estimated that approximately 1,000 acres were being censused. Field No. 23, containing 130 acres, represented 13 per cent of the area covered. Thus, 11 per cent of the hares were being seen on approximately 13 per cent of the area, indicating that the hare density in field No. 23 was probably comparable to the density over the remainder of the area. Accordingly, the number of hares on the management area west of, and including, field No. 27, was estimated to be about 1,100 in the late fall of 1955.

Unfortunately, there are no figures available for densities of jack rabbits at other locations in similar habitats. Brown (1947) reports their density to be about 1 per acre on mixed prairie near Hays, Kansas. Wooster (1935), working in the same type of habitat, reports an increase from 159 per square mile in 1933 to 484 per square mile in 1935. Biswell, *et al.* (1952) indicate populations of about 10 to 45 per square mile in open brush and about 1 per square mile in dense brush in Lake County, California. There are many reports of jack rabbit abundance on the desert. Vorhies and Taylor (*op. cit.*) indicate a population of about 0.234 per acre on the Santa Rita Range in Arizona. Fautin (1946) reports a maximum population of about 0.22 per acre in a shad scale association near White Valley, Utah. Woodbury (1955), using a drive census, reports about 0.43 per acre in the Great Salt Lake desert area of Utah. Thus, it appears that the jack rabbits on the Gray Lodge Waterfowl Management Area are as abundant as those on any other area recently reported, and more abundant than on most areas. However, these densities seem low when compared to those of some of the counties in southern California in the latter part of the last century. Palmer (1897) lists many instances of jack rabbit densities greatly in excess of 1 per acre. For example, he reports that in the San Joaquin valley near Bakersfield between the second and tenth of January 1888, 8,000 jack rabbits were killed in less than 1 square mile!

MORTALITY

Table 1 gives an idea of the rate of loss of the trapped hares in the red and yellow areas. In constructing the table, data from the hares in the blue area were omitted because of insufficient observations. The losses indicated by Table 1 might be due to emigration, loss of tags, or mortality.

TABLE 1.—THE NUMBER OF JACK RABBITS MARKED AND SUBSEQUENTLY OBSERVED OVER A 17-MONTH PERIOD[1]

1954–55	1955				1955–56		1956
Nov.–Jan.	Feb. Mar.	Apr. May	June July	Aug. Sept.	Oct. Nov.	Dec. Jan.	Feb. Mar.
5	3	1	1	1	1	1	1
–	5	3	2	2	2	2	2
–	–	6	4	3	3	3	3
–	–	–	3	1	1	1	1
–	–	–	–	4	4	4	3
–	–	–	–	–	38	30	19

[1] The first number in each horizontal series represents the number of animals marked in that period, and the remaining numbers represent the number of these subsequently observed.

Emigration was apparently slight for, except during the flood, no hare was seen over ¾ mile from where it was marked.

There was no known case of tag loss throughout the study. The tags on recaptured and dead hares were all in excellent condition. The first hare tagged was seen at the end of the study about 16 months later. The discs on one ear and the tattoo on the other ear were still visible. If tag losses occurred, they were a minor factor in the disappearance of the marked animals.

This leaves mortality as the major factor affecting the disappearance rate of the jack rabbits. One of the most striking things that can be seen in Table 1 is that there were hares alive at the end of the study from each of the marking periods. Although hares disappeared during each of the periods, the greatest losses occurred in the winter months of January, February, and March. It

appears that the hares that survived this period had a good chance of living for the remainder of the year. The sharp loss of hares in the December–January period of 1955–56 is probably a reflection of the flood.

Carcasses of hares were found on the management area west of fields Nos. 27 and 16 (Fig. 4) throughout all months of the study, but they occurred in greatest numbers during the fall and winter. Excluding hares killed by automobiles, 150 carcasses were found. The sex ratio of 114 of these was 53:47, indicating that mortality was equally distributed between the sexes.

By far the greater number (116) of the carcasses were found during the flood period of January and February 1956. At this time, the hares were forced into a much reduced area where it was hard for them to find food and cover when weather conditions were adverse. Increased contacts between individuals undoubtedly facilitated the spread of infection, and they were constantly harassed by dogs and humans.

Ninety-seven of the carcasses found during the flood were aged. The age distribution of this sample was similar to that of a sample of hares shot during these same months, indicating that mortality was spread equally among hares of various ages.

The carcasses of four of the marked animals from the red area were found during the flood. From observations on marked hares before and after the flood, it was estimated that 16 marked animals had disappeared from this area during the same period. Assuming that the chances of finding a marked or unmarked carcass were the same, it would appear that only ¼ of the total carcasses available were found. Thus, the number of deaths on the management area west of, and including, field No. 27 was probably close to 400 out of a population of approximately 1,100, indicating a loss of almost ⅓ of the hares in a 2-months' period.

Possible Causes of Mortality

Road Kills

Automobiles kill a large number of jack rabbits. During the study, over 100 carcasses were found on roads of the management area and on rural highways leading to the towns of Gridley and Live Oak. The age classes and sex ratio of these carcasses were similar to those of the study population, and no differential mortality could be detected.

Fire

In the spring, many of the fields on the management area and the surrounding farm lands are burned to eliminate weeds and crop stubble preparatory to planting. These fires may take a great toll of jack rabbits, especially the young of the first litters. Many hares in the kill collections in early spring had badly singed fur. Observations revealed that the jack rabbits are not adept at avoiding fire, and many of them were seen to run directly through the advancing wall of low flames. None of the scorched hares seemed to be seriously burned, but it is reasonable to assume that some are lost in this manner, especially when the fires are extensive and hot.

Predators

Of the predators on the management area, only dogs seem to kill adult jack rabbits in any numbers. Six instances were noted of dogs killing adult hares. Dogs appear to be efficient killers of jack rabbits, especially when they work in pairs or groups. During times that are adverse for hares, such as during the flood, dogs could exert a considerable drain on the population.

Feral house cats were abundant on the area. Many times cats passed within a few feet of feeding jack rabbits, but neither seemed to notice the other. Cats probably find and kill some of the very young hares.

Raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*) were common on the management area. I feel that they have little or no effect on the adult jack rabbits but may eat the young.

Ten species of hawks and owls were seen on the study area. The jack rabbits paid little or no attention to any of these birds, and none of them was ever known to kill jack rabbits.

Garter snakes (*Thamnophis sirtalis*) and gopher snakes (*Pituophis catenifer*) occur

on the area and probably eat young jack rabbits. Chester M. Hart (pers. comm.) noted and photographed a gopher snake in the process of consuming newly born jack rabbits.

Almost all of the animals listed above may at times eat jack rabbits, but I doubt that they have any appreciable influence on the jack rabbit population. From observations in this study, it appears that evaluations of predation based on examination of the stomach contents of predators should be viewed with skepticism, for, although most of these predators were never known to kill hares, they were seen many times feeding on carcasses of jack rabbits that had been killed by some other means.

Parasites and Diseases

A variety of parasites and infectious diseases were detected in the jack rabbit population, but since only tularemia and coccidiosis are suspected of causing mortality they are the only ones discussed here.

Tularemia.—During the study, eight carcasses of jack rabbits were found that had small, round, white lesions on the liver and spleen. Three of these were found in December 1954, three in February 1955, one in January 1956, and one in February 1956. No bacterial isolations were made from any of these animals, but pieces of the livers were preserved and later sectioned and stained. They showed necrotic lesions with some cellular infiltration and could have been caused by an infection with *Pasturella tularense*. However, positive diagnosis cannot be made on this basis. Although these could have been individual cases of tularemia, the time of occurrence seems strange, for all took place during the low point in the abundance of known vectors such as ticks and flies. It could be that, because of the low incidence of vectors, the disease was more or less isolated in a few hares and did not reach epidemic proportions. Occurrences of tularemia in rabbits and hares are known to be sporadic, and it has been demonstrated that arthropods, such as ticks, serve as reservoirs as well as vectors. Thus, there is a constant possibility that the disease may flare into epidemic proportions at any time when the vectors become abundant.

The public should be informed of the danger of the disease and of preventive measures against it. Any obviously sick or distressed hares should never be handled and all jack rabbit meat should be thoroughly cooked before it is eaten. The logical time to harvest the jack rabbits on the Gray Lodge Waterfowl Management Area is in the fall when the area is open to the hunting of ring-necked pheasants (*Phasianus colchicus*). At this time the arthropod vectors of tularemia are at a low ebb and the jack rabbits are predominantly young of the year. Any widespread die-off of the jack rabbits would probably soon be detected by management personnel and, under such circumstances, hunting of jack rabbits could be prohibited.

Coccidiosis.—Examination of caecal contents of the jack rabbits collected throughout the year showed that over 90 per cent of them had coccidian oocysts present. No attempt was made to identify these as to species, but since they varied in size and form, and since no other genus has been reported from rabbits or hares, they probably represent various species of *Eimeria*. No cases of gross lesions of the liver or intestines due to coccidia were noted in the kill sample. During the flood, about 20 per cent of the dead jack rabbits found had multiple, pinhead-sized, white lesions in the small intestines. Histological sections of these intestines showed numerous stages of coccidians. The lesions were considered extensive enough to have been the major factor in the death of the hares.

It appears that only during the flood period when the hares were crowded into wet, unsuitable environments did these parasites become a factor in the mortality of the jack rabbits. What role they may play in more normal times is not clear, but from the hares examined in this study it appears to be slight.

Shock disease.—Although about 20 per cent of the jack rabbit deaths during the flood could probably be attributed to coc-

cidiosis, the majority could not be explained by any causative agent. Drowning was not a major factor, since most of the dead hares were found on the levees and roads above the level of the water. No gross lesions were noted on most of the carcasses, and the incidence of parasites, other than coccidians, was not higher than in the animals collected earlier. At necropsy the majority of the carcasses showed mahogany-red livers, and there were frequent cases of hemorrhage about the adrenals. Many of the adrenals appeared to be enlarged, but no measurements were taken.

Several of the carcasses were found in a position typical of that described by Green and Larson (1938) and shown by Green, Larson, and Bell (1939, Fig. 1) for snowshoe hares (*Lepus americanus*) that had died of "shock disease." In the present study, one hare was found lying on its side. It was extremely "bug-eyed" and moribund, but occasionally made running motions with its feet. At the same time, there was a continuous raising and lowering of its head, accompanied by gasping. It died with its extremities extended, and rigor mortis set in almost immediately. Similar symptoms had been observed in a trapped animal that later died. Another trapped animal died rather suddenly while being handled, to all appearances being "scared to death." Neither of these animals showed bodily damage from fighting the trap, as did others found dead in the traps.

These symptoms and post-mortem findings are similar to those of the shock disease of Green and Larson (*op. cit.*) or to those of the diseases of adaptation of Selye (1946). It is entirely possible that during the flood, when the jack rabbits were subjected to a great variety of stresses such as wetness, cold, lack of suitable food and cover, crowding, and increased alarm stimuli from harassment by humans, dogs, and others, there may have been an exhaustion of the adrenopituitary system of some of them, resulting in hypoglycemic shock and death. The fact that both sexes and all age classes were affected agrees well with the findings of Green and Larson (*op. cit.*) and adds further support to the hypothesis that the majority of the flood deaths were due to shock disease or the adaptation diseases of Selye.

SUMMARY AND CONCLUSIONS

A population of the black-tailed jack rabbit was studied on the Gray Lodge Waterfowl Management Area, Butte County, California, from October 1954 to March 1956. Two methods were used: one of these consisted of the necropsy of a number of hares killed in each month of the study period; the other consisted of capturing, tagging, releasing, and then observing a sample of the hares.

A total of 677 trap nights resulted in the capture of 143 jack rabbits; 100 were tagged and released. Numerous observations on the tagged jack rabbits indicate that these hares have rather well-defined home ranges of less than 50 acres. There is considerable overlap of individual home ranges at the observed density of about one jack rabbit per acre. The size of the home range seems to be determined by the pattern of food, water, and cover in the environment. Shifting, expansion, and contraction of the home ranges allow for the quick population of fields that were formerly not suitable habitat. Jack rabbits driven from their home ranges may return to them.

Automobiles and fires may kill considerable numbers of jack rabbits. Predators, except dogs, appear to have little influence on the adult population. The greatest losses of marked jack rabbits occurred in the winter. During and after the winter flood of 1955–56, 150 carcasses were found. About 20 per cent of these deaths were probably due to an intestinal coccidiosis, but the remainder appeared to have died of a condition resembling shock disease.

LITERATURE CITED

BISWELL, H. H., R. D. TABER, D. W. HEDRICK, AND A. M. SCHULTZ. 1952. Management of chamise brushlands for game in the north coast region of California. Calif. Fish and Game, 38:453–484.

BROWN, H. L. 1947. Coaction of jack rabbit, cottontail and vegetation in a mixed prairie.

Trans. Kansas Acad. Sci., 50:28–44.

BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal., 24:346–352.

FAUTIN, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr., 16:251–310.

GREEN, R. G., AND C. L. LARSON. 1938. A description of shock disease in the snowshoe hare. Amer. J. Hyg., 28:190–212.

GREEN, R. G., C. L. LARSON, AND J. F. BELL. 1939. Shock disease as the cause of the periodic decimation of the snowshoe hare. Amer. J. Hyg., 30:83–102.

LEOPOLD, A. 1933. Game management. New York: Charles Scribner's Sons. 481pp.

ORR, R. T. 1940. The rabbits of California. Calif. Acad. Sci., Occ. Papers, No. 19:1–227.

PALMER, T. S. 1897. The jack rabbits of the United States. U.S. Dept. Agric., Div. Biol. Surv. 88pp.

SELYE, H. 1946. The general adaptation syndrome and the diseases of adaptation. J. Clin. Endocrin., 6:117–230.

TYNDALE–BISCOE, D. H. 1953. A method of marking rabbits for field studies. J. Wildl. Mgmt., 17:42–45.

VORHIES, C. T., AND W. P. TAYLOR. 1933. The life histories and ecology of jack rabbits *Lepus alleni* and *Lepus californicus* ssp. in relation to grazing in Arizona. Univ. of Ariz. Agric. Exp. Sta., Tech. Bull. No. 49:471–587.

WEBB, W. L. 1942. Notes on a method for censusing snowshoe hare populations. J. Wildl. Mgmt., 6:67–69.

WOODBURY, A. M. 1955. Ecology of the Great Salt Lake desert. I. An annual cycle of the desert jack rabbit. Ecology, 30:353–356.

WOOSTER, L. D. 1935. Notes on the effects of drought on animal populations in western Kansas. Trans. Kansas Acad. Sci., 38:351–352.

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FOOD HABITS OF THE NEWFOUNDLAND WILLOW PTARMIGAN

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The population of Newfoundland willow ptarmigan, *Lagopus lagopus alleni* (Stejneger, 1884) has decreased considerably in recent years. The reason for this decline is the object of an intensive research program by the Wildlife Division of the Newfoundland Department of Mines and Resources.

This paper deals with food habits and encompasses field observations and the analysis of crops and droppings of willow ptarmigan, mainly from the Avalon Peninsula, from the fall of 1954 through the fall of 1956. Quantitative comparisons between available vegetation and food items selected by the birds are also discussed. Most of the crops were from birds collected during the regular October hunting seasons by cooperating sportsmen, who provided field information and anatomical parts from their bagged birds. The present scarcity of willow ptarmigan prevented all but meagre collecting at other times of the year.

Former food-habits studies conducted in Scotland and Norway on the genus *Lagopus* by Wilson and Leslie (1911), Holmboe (1924), and others, clearly indicate that these birds are closely associated with an ericaceous flora. Inventories of the Avalon Peninsula flora, to determine the relative abundance of possible food and cover species, were conducted by the writer and by Eli Lear in 1955 and more extensively during the summer of 1956 by Lear. A reference collection was made for comparative purposes in crop-content analysis.

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AREA OF INVESTIGATION

The Avalon Peninsula is a dissected plateau of about 4,000 square miles with an average elevation of 700 feet above sea level. It is the most easterly part of the Province of Newfoundland, and separated from the main part of the island by an isthmus narrowing to about 2 miles in width. Because of four large bays, there is no part of the peninsula more than 15 miles distant from the Atlantic Ocean. The coast line is indented by numerous fiords and bays characterized by sheer cliffs from 300 to 500 feet high. The surface is rocky, interspersed with over 1,400 square miles of tundra-like barrens. Drainage is poor, with innumerable short streams that course between shallow depressions containing small lakes and bogs. Although the area lies within the boreal forest region, the cold Labrador Current causes a generally cold climate, which is unfavourable for good tree growth. In the sheltered areas, however, the shallow, acid podzolic soils support a moderate growth of spruce and fir and an excellent growth of many species of ericaceous plants.

Strong winds and gales (over 33 m.p.h.) are common but occur more frequently during winter. They keep the exposed hills swept free of snow but cause deep drifts in the many gorge-like valleys and low crags. There is a yearly snowfall of about 100 inches. Because of the influence of the ocean, variations in temperature are limited, seldom ranging through more than 35°F. Midwinter temperatures do not fall much below freezing. The persistent thaw (mean temperature above 32°F.) occurs between April 5 and 10. The duration of the growing season, i.e., when the mean air temperature remains above 43°F., is between 150 and 160 days, commencing in the latter half of May and ending in October. There are about 130 frost-free days annually. Summers are short but pleasant, with a mean July temperature in the 50's. Annual rainfall of between 50 and 60 inches provides a moisture surplus of more than 30 inches, i.e., precipitation exceeding water consumption by evapotranspiration (Hare, 1952). Fogs are common all year but are particularly frequent during April, June, and November.

The interior of the Avalon Peninsula is uninhabited, but residing in coastal settlements are nearly half of Newfoundland's estimated population of 415,000, including a large number of sportsmen. With only a small population of caribou (*Rangifer caribou*) and moose (*Alces alces*), which may never support a legal harvest because of a very restricted habitat, and with a present low of varying hares (*Lepus americanus*), the bulk of the hunting pressure is borne by the willow ptarmigan, the only upland game bird.

METHODS AND TECHNIQUES

Although intensive research was not begun until the spring of 1955, crops were obtained from the 1954 hunting season so that an early appreciation of food requirements might be established. The only information accompanying these crops was the locality and date of collection. As field work progressed in 1955, it was evident that, due to the scarcity of ptarmigan, sufficient material for a food-habits study would have to come from fall-shot birds, provided mainly by hunters.

Co-operators were provided with printed instructions and all materials, save hunting equipment, needed for collecting specimens. On numbered crop tags, they were requested to record date, locality, and time of kill, and, in 1956, the number of birds in each covey encountered. Stamped, return-address envelopes were used for the wings, and sometimes the tail, of each bird. At the time the wings were enclosed, the crop-tag number was recorded on the envelope, or, in some cases, a wing tag bearing a duplicate of the crop tag was inserted with the wings. Crops were individually wrapped in cheesecloth, tied with the tags affixed and immersed in a solution of 5 per cent Formalin.

In the laboratory the crops were opened and the wet contents emptied into graduated cylinders. Any surplus water was drained off and a measured amount was then added; the displaced volume was recorded. The cylinder contents were then emptied into a funnel in which filter paper had been placed. After draining, but with contents still wet, the filter paper was unfolded on a shallow dish and the contents sorted. The various items were identified and measured volumetrically to the nearest 0.1 ml. When items were recorded on data sheets, those with a volume of less than 0.1 ml. were treated as traces. Grit and animal matter, when present, were handled in the same way as other items. A reference collection of crop items, which were enclosed in a Nasco seed mount (style S–6), greatly expedited the subsequent identification of some of the less frequent and confusing items.

The value of working with damp crop contents facilitated the identification of leafy material such as frond fragments of *Dryopteris* and leaf fragments of *Prenanthes*. Animal matter, such as small soft-bodied larvae, might easily have been overlooked if dried. With ptarmigan, where pulpy berries like *Vaccinium* spp. may sometimes comprise the bulk of the crop contents, the significance of these items depends on their evaluation while still turgid, whether they are weighed or measured volumetrically. Although an air-dried method of analysis was tried, there were so many unrecognizable items that it was abandoned. This paper deals only with data based on handling moist material.

The crop data were tallied and the volumes totaled for each classified food item found in the crops for each locality and season. Frequencies of occurrence for each item, including traces, were also totaled. These data were, in part, summarized by the aggregate volume method as described by Martin, Gensch, and Brown (1946).

Droppings were usually analyzed in the field with the aid of a 10× hand lens during regular field investigations. They were crushed and loosened by rolling them between the thumb and fingers, or, if very fibrous, pulled apart over a shallow receptacle. The fibers, bud scales, seeds, and other items were identified and recorded by frequency of occurrence. Presence of grit was noted. Collections were occasionally made for more detailed microscopic analysis. A reference collection of droppings from captive ptarmigan was obtained by feeding them specific food items.

Preliminary analysis of the contents of gizzards and lower alimentary tracts of the few ptarmigan collected was found not to add to food-habit knowledge gained from crops, and these organs were subsequently used only for parasitological investigations. The problem of making arrangements for rapid fixation after collecting made it impractical to solicit alimentary tracts.

To determine the Avalon flora, point-transect and metre-quadrat plots were generally used in 1955. Lear, during 1956, made 20 sample-plot (1 by 0.1 metre) readings on 50 stations. Plants were recorded by frequency of occurrence and percentage of ground cover. During the two years, over 1,300 plots were inventoried. Scientific and common names of plants listed in this paper follow those used by Rouleau (1956).

FLORAL SURVEY IN PTARMIGAN HABITAT

Table 1 lists, in decreasing order of abundance, the ten most prevalent plants found on the Avalon Peninsula barrens, and the importance of each as a food source for the willow ptarmigan during fall.

Except in the bogs, *Vaccinium angustifolium* and *Kalmia angustifolia* are the two most abundant and widely distributed plants found on this ptarmigan range. Although the two plants occur together, there are vast areas that appear to favour the growth of *Kalmia*. Some of these sites indicate that *Kalmia angustifolia* has recently suppressed *Vaccinium* spp. and some other less abundant but desirable ptarmigan food species. We have no history of the former distribution or abundance of *K. angustifolia* but, from interviews with sportsmen and our own field observations, it appears to be on the increase.

TABLE 1.—COMPARISON BETWEEN THE TEN MOST ABUNDANT PLANT SPECIES OF THE BARRENS, AND THE AMOUNT OF FALL UTILIZATION BY PTARMIGAN

Column A: Plant inventory (1,300 plots during 1955 and 1956)
F = per cent frequency of occurrence.
C = per cent ground coverage.
Column B: Crop analysis (223 crops from fall 1954, 1955, and 1956)
F = per cent frequency of occurrence.
V = per cent aggregate volume

Plant Species	A		B	
	F	C	F	V
Vaccinium angustifolium	92	18	84	47
Kalmia angustifolia	85	19	—	—
Vaccinium Vitis-Idaea	78	6	27	7
Cornus canadensis	76	6	1	tr.
Empetrum nigrum	27	12	16	2
Ledum groenlandicum	36	3	9	tr.
Maianthemum canadense	46	2	1	tr.
Potentilla tridentata	43	2	28	7
Deschampsia flexuosa	27	2	7	tr.
Trientalis borealis	36	1	—	—

There are several large expanses of the Avalon Peninsula where there is no tree cover. There are other large areas that are completely covered by a dense prostrate stand of black spruce (*Picea mariana*). This situation, from the standpoint of attracting ptarmigan, is less favourable than the treeless areas. The most desirable habitat is where there are small island-like stands of *P. mariana* and balsam fir (*Abies balsamea*), locally called "tuckamores," interspersed with the ericaceous barrens. These tuckamores, or "tucks," are used extensively by ptarmigan throughout the year. A bird flushed from open barrens will usually fly to the nearest tuck for cover. *Larix laricina* does not usually form tuckamores but is found in bogs as dwarf plants and as scattered small trees around the edges.

FEEDING HABITS

During the summer, fall, and winter of 1955 and the spring and summer of 1956, many predawn vigils were made on areas frequented by ptarmigan. Willow ptarmigan have been seen feeding in the morning as soon as there was enough light to make observations. Unless disturbed, they will usually commence their feeding in the vicinity of where they spend the night. Heavy rains, winds, and other adverse weather appear to modify their daily feeding habits, for they have been observed to range less in foraging during these periods.

Nearly all their food is vegetable matter; but when insects are plentiful, it is not unusual to see adult birds snap at, and apparently swallow, various flies and mosquitoes. Insect larvae are also eaten, but usually only in trace amounts, although one bird collected outside the Avalon Peninsula had eaten over 50 large lepidopterous (Noctuidae) larvae. Christiansen and Krafft (1953) found that insects form an important part of the diet of Norwegian ptarmigan chicks, particularly during the first ten days. Grimshaw (1911) found that, although insects are commonly eaten by Scottish red grouse (*Lagopus scoticus*) chicks, many crops examined during the grouse study in Great Britain contained no trace of them. No very small Newfoundland ptarmigan chicks were collected during this study, but observations and experimentation on captive chicks through two seasons led to the following conclusions: Young ptarmigan are more insectivorous than are the adults, but take plant items as soon as they are physically able. A chick's strength, size, weight (hatching weight = 15 to 17 grams), and the relatively soft nature of the mandibles limit their feeding habits to small animal life, and to the less ligneous parts of plants, such as blossoms and new small leaves. Within a few weeks, however, they become adept at rapidly snipping off twigs up to 2 mm. in diameter, the clicking of their mandibles being audible for several yards.

Most feeding is done in a rapid snipping fashion. An entire twig may be consumed by a series of rapid small bites, each bird using the cutting edge of only one side of its bill. During this "snip-feeding," the nictitating membrane is drawn across the cornea almost rhythmically with the actual bite. Berries are rapidly picked and gulped down, usually without puncturing the skin. Small leaves are swallowed whole, but large leaves are eaten by a series of bites in a

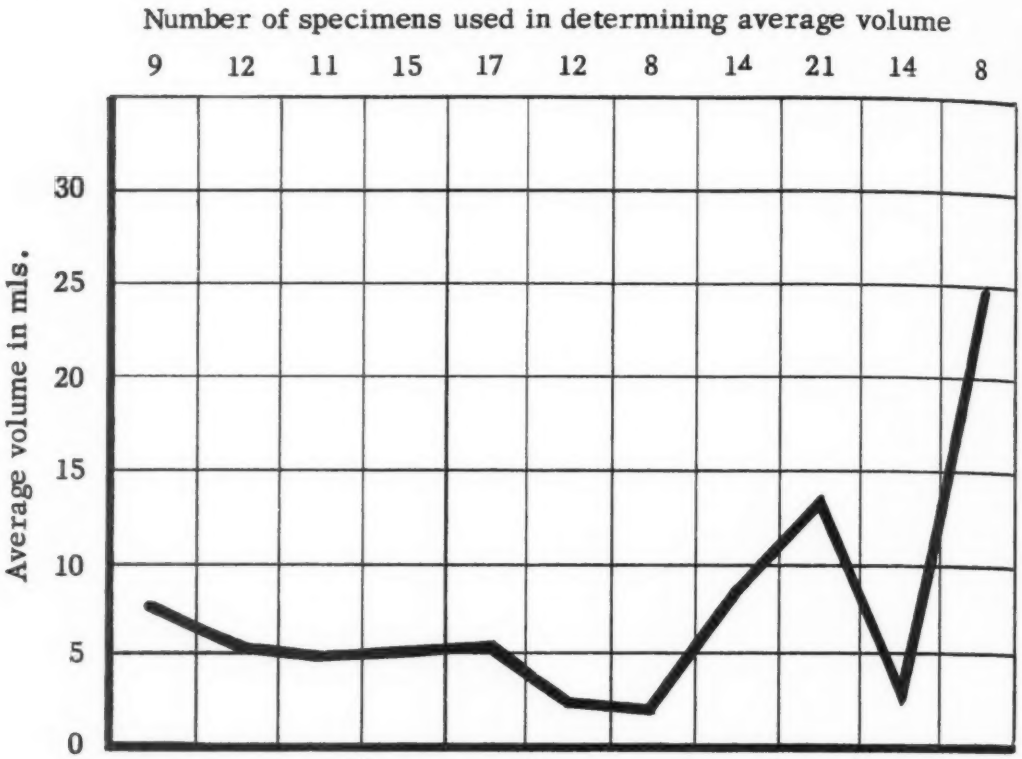
Number of specimens used in determining average volume
9 12 11 15 17 12 8 14 21 14 8
Average volume in mls.
0 5 10 15 20 25 30
7 8 9 10 11 12 1 2 3 4 5 6
Time of day

FIG. 1. Average hourly crop volume (mls.) based on 141 willow ptarmigan collected during October 1955 and 1956.

tearing fashion. If the leaf should break off during this process, while still too big to swallow, it is quickly discarded, for even adult birds are unable to take a bite out of a thin leaf unless it is attached.

The buds, twigs, small stems, leaves, blossoms, and fruit are eaten from *Vaccinium* spp. Some other plants have only one specific part used as a food item. Among 223 age-classified crops containing food (average volume 10.3 mls.) and collected during October, 60 food items were represented. Each plant part, i.e., buds, twigs, leaves, and fruit, if occurring separately and in more than trace quantities, constituted a food item in this study. From these crops, it was found that adult birds consumed 34 of these items, whereas the young of the year ate 54 of the 60 food items recorded. Even when one includes animal matter, most of the 23 items eaten by young and not by adults were only of trace proportions. The four items eaten only by adults could, with the exception of *Polygonum* sp. seeds, be classed as accidental ingestion. Although this possibility could not be ruled out in explaining some items found in young-of-the-year crops, it does, however, suggest that there is a long period of experimental sampling for preferred food items by young birds.

The intake of food during the morning is apparently little more than what can be digested (Fig. 1). The Scottish red grouse follow the same pattern, as reported by Wilson and Leslie (*op. cit.*). Around noon, feeding activity is reduced. With the captive birds, this time appeared to be a definite rest period. The conclusions of Krafft (1954) on the feeding times of Norwegian

ptarmigan chicks, based on crop contents, closely parallels our conclusions based on older birds. He found that chicks had a rest period at noon. In early afternoon, feeding is resumed at a greater rate, but is again intensified during late afternoon. From this late-afternoon peak until feeding stops for the night, presumably at dusk, the food intake is sufficient to maintain engorged crops. During this period, it is common to collect birds with crops containing more than 40 ml. of food material. One immature ptarmigan had a crop containing 79 ml., including, besides a sizable list of other items, 191 berries, 640 twig fragments and buds, and 21 leaves taken from *V. angustifolium*.

The apparent additional rest period around 4 P.M., indicated by Fig. 1, is not substantiated by field observations, nor by activity periods of captive birds. As these data for Fig. 1 were obtained during the hunting season, there is a possibility of a disturbing influence affecting normal feeding habits, but hunting pressure is not accelerated at this time of day. Although this graph is an aggregate of 2-years' data, graphs constructed from data for each year, and between adults and young, still show the same 4 P.M. slump in crop volume.

GRIT AND WATER

The importance of grit to the welfare of *Lagopus* spp. is emphasized in papers by Hammond-Smith and Rastall (1911) and Kolderup (1924), the limiting factor being the availability of grit during the winter, when the usual source is cut off by snowfall. This situation probably is rare on the Avalon Peninsula, where there are usually plenty of exposed fragmented rocks throughout the year.

Kolderup (*ibid.*), in his Norwegian studies, found that gizzards from willow ptarmigan contained less grit by number and weight during winter than during summer. He attributed this to availability. The frequency of grit appearing in the droppings of ptarmigan on the Avalon Peninsula, where there appears to be no problem of supply, was also less during winter.

Ptarmigan can apparently get along quite well on a less-than-normal quantity of grit in the gizzard and have the ability to retain this reduced amount long after the source of supply is cut off (Kolderup, *ibid.*). Hammond-Smith and Rastall (*op. cit.*) report that a Scottish grouse died on the twenty-first day of experimental grit starvation, as a result of losing, through the normal process of digestion, about half of its original supply. Kolderup (*op. cit.*) does not feel that this was the reason for death. No grit experimentation was conducted on our captive birds. Although grit is not regularly found in the crops, as many as five grains have been recorded during the investigation. Most of the grit found was also equal in size to the largest ones found in the gizzards, suggesting that small gizzard grit is the result of abrasion.

That the hard seeds from *Rubus Chamaemorus, Cornus canadensis,* and *Maianthemum canadense* are sometimes substituted for grit is suggested from the examination of several gizzards, examined by the author, from fall-shot ptarmigan that contained many of these seeds and only a few grains of grit. These seeds also showed differential wear, and the gizzard was the only place in the alimentary tract where they were found. Smaller *Vaccinium* spp. seeds, and sometimes those of *R. Chamaemorus, C. canadensis,* and *M. canadense* pass through the gizzard without showing any sign of abrasion. It seems reasonable that these hard seeds could function as grit during the time of year when pulpy fruit is consumed in large quantities. Although some pieces of grit are considerably larger than the seeds from these three plants, there is far more grit in the average gizzard that is smaller.

Water is not considered to be a problem for Newfoundland ptarmigan. Although water is easily secured throughout most of the year, I have observed that, when quantities of berries are eaten, the birds drink less. This has been experimentally demonstrated with the captive birds. If, during the winter, the usual water source is frozen, the birds, both captive and wild, readily

TABLE 2.—PRINCIPAL FALL FOOD ITEMS EATEN BY NEWFOUNDLAND WILLOW PTARMIGAN[1]

1954: 80 crops, 11 empty, average crop volume 11.6 ml.
1955: 66 crops, 16 empty, average crop volume 12.4 ml.
1956: 119 crops, 15 empty, average crop volume 6.9 ml.

Plant Species and Part Taken	Freq. of Occur. (Per Cent)	Aggreg. Volume (Per Cent)
SPECIES BEARING FLESHY FRUITS		
Empetrum nigrum		
fruit	9	2
plant tips	9	tr.
Gaylussacia baccata		
fruit	15	11
leaves	tr.	tr.
Maianthemum canadense		
fruit	1	tr.
Pyrus arbutifolia		
fruit and/or buds	2	tr.
Rosa nitida		
fruit	1	tr.
Rubus Chamaemorus		
fruit	5	tr.
Vaccinium angustifolium[2]		
fruit	73	37
leaves	42	3
buds and twigs	62	8
Vaccinium Oxycoccos		
fruit	22	9
stems and leaves	28	4
Vaccinium Vitis-Idaea		
fruit	23	6
leaves	13	tr.
buds and twigs	4	tr.
Viburnum cassinoides		
fruit	4	tr.
SPECIES BEARING CAPSULAR FRUITS		
Andromeda glaucophylla		
capsules	11	1
leaves	8	tr.
Chamaedaphne calyculata		
capsules	26	3
buds	1	tr.
Kalmia polifolia		
capsules	3	tr.
Ledum groenlandicum		
capsules	9	tr.
leaves	1	tr.
Rhododendron canadense		
capsules	2	tr.
buds and twigs	5	1
OTHER SEED-BEARING SPECIES		
Betula pumila[3]		
staminate catkins	5	tr.
pistillate catkins	3	tr.
buds & twig fragments	11	tr.
leaf fragments	3	tr.
Carex sp.		
seeds	5	tr.
Deschampsia flexuosa		
spikelets	7	tr.
Polygonum sp.		
seeds and stem	2	tr.
Potentilla tridentata		
seed heads	28	7
Prenanthes trifoliolata		
heads	10	3
leaf fragments	4	tr.
Rhynchospora alba		
seeds and stem	7	tr.
Salix sp.		
buds & twig fragments	1	tr.
Scirpus cespitosus		
seeds	14	tr.
Trifolium sp.		
seed pods	1	tr.
OTHER VEGETATION		
Equisetum arvense		
fragments	2	tr.
Dryopteris spinulosa		
frond fragments	6	tr.
Polystichum sp.		
frond fragments	3	tr.
Schizaea pusilla		
fruiting fronds	3	tr.
ANIMAL MATTER		
Ichneumonidae		
wasps	3	tr.
Oniscidae		
sow-bugs	3	tr.
Noctuidae		
larvae	1	tr.
Tenthredinidae		
saw-fly larvae	2	tr.

[1] Species with both frequency and volume values of 0.5 per cent or less have been deleted from table for sake of brevity. The percentages in the table are calculated to the nearest whole number and items with a value of 0.5 or less appear as traces (tr.).

[2] Including small amounts of *V. uliginosum*.

[3] Including some *Betula Michauxii*.

eat snow. Snow is also used as a medium for a winter "dust-bath."

FOOD ITEMS TAKEN

During early fall, berries comprise the bulk of ptarmigan food, and blueberries (*V. angustifolium*) make up over half of the total berry consumption. Other important berries are *V. Vitis-Idaea, V. Oxycoccos, Gaylussacia baccata,* and *Empetrum nigrum.* A 3-year aggregate breakdown of the most important fall food items (based on volume and frequency of occurrence) eaten during 1954, 1955, and 1956 appears as Table 2.

As fall progresses, the fruit and leaves fall off the *V. angustifolium* bushes, and concurrently there is a transition to a more ligneous diet of buds and twigs that becomes more evident as winter approaches. The drop in berry consumption and the simultaneous disappearance of fruit from *V. angustifolium* bushes is probably only coincidental, as there is still abundant fruit on *V. Vitis-Idaea, V. Oxycoccos,* and *E. nigrum* available to the birds. Possibly, as Gelting (1937) suggests, there is a change to a higher caloric intake in selecting winter foods higher in protein. Gelting (*ibid.*) found that nutritional needs not only governed the intake of specific foods of the Greenland ptarmigan, but also prompted mass movements, one of which he called a "protein migration."

The winter diet of Avalon ptarmigan is almost exclusively of buds and twigs of *Vaccinium* spp., buds and catkins from *Betula* spp. and *Alnus* spp., and buds of *Myrica Gale* (the only time this plant has been found as a food item). I have observed willow ptarmigan feeding on the capsules and buds of *Ledum groenlandicum* and *Rhododendron canadense,* but recognizable fragments have not been seen in the droppings. Several crops from rock ptarmigan (*Lagopus mutus*), collected on Newfoundland's west coast, were engorged with *R. canadense* buds.

In Norway, Nordhagen (1928) reports that availability is a factor in determining what is eaten by ptarmigan. In the interior of Norway, where deep snow covers the ericaceous plants, the willow ptarmigan subsists on the buds and catkins of birches and willows. Along the coast, on the other hand, where there is considerably less snow, the ericaceous plants are considered to be important winter foods, along with the birches and willows.

On the Avalon Peninsula, ptarmigan are seldom restricted by snow or other weather conditions to a particular diet. It has been reported by local residents, but unsubstantiated, that sleet storms (locally called "glitters") have occasionally resulted in mortality from starvation. This situation is considered to be rare. Therefore, barring an extensive "glitter," the selection of winter foods is most likely governed by the physiological needs of the birds.

During the spring, there is a return to a diet consisting of more fruit and leafy material. At this time, berry seeds of *E. nigrum* and *Vaccinium* spp. (probably *V. Vitis-Idaea*), from fruit that remained on the plants all winter, appear in the droppings. As summer approaches, the new vegetative growth is used as food. On June 22, the crop of an incubating female contained 8 ml. of only the leaves of *V. Vitis-Idaea.*

During July and August, the droppings of both adults and young are often stained with berry juice, and *Empetrum* seeds are commonly found in them. The crop of a young bird collected on July 16 contained frond fragments of *Dryopteris* and seeds of *Carex* spp. An adult male collected the same day had eaten fragments of *Dryopteris,* spore capsules of a moss (*Polytrichum*), 15 berries of *V. Vitis-Idaea,* and approximately 60 berries and some leaves from *V. angustifolium.*

An adult male collected on August 1 had 62 *E. nigrum* berries and over 100 *V. angustifolium* leaves in its crop. An immature male collected the same day had eaten 9 *E. nigrum* berries, one fly, and a small lepidopterous larva. Between August 8 and 10, eight 5- to 6-week-old chicks were collected during midday, and all had empty crops. A young bird collected earlier in the morning of August 13 had eaten 2 ml. of

E. nigrum berries, besides mosquitoes, spiders, two small flies, one wasp, and a small lepidopterous larva. Two adults taken later in the month had eaten fruit and leaves of *V. angustifolium*, fruit of *G. baccata*, and some heads from *Prenanthes trifoliolata*.

In discussing the food of Newfoundland willow ptarmigan, Bent (1932) quotes J. R. Whitaker: "In August the blueberries and partridgeberries (*Mitchella repens*) ripen and on these they feed almost exclusively." The partridge berries of Newfoundland are not *M. repens*, but *Vaccinium Vitis-Idaea*. I suggest, therefore, that in view of the rareness of *M. repens* in Newfoundland and the possible misinterpretation of a vernacular plant name, this plant should be considered as *V. Vitis-Idaea*.

According to Nordhagen (*op. cit.*) and our observations, berries are eaten as soon as they appear, and before they are ripe. Olstad and Lid (1923) found that the quantity of berries eaten by ptarmigan depended primarily on the nature of the berry crop, implying that berries are an important food when available. The importance of an abundant supply of berries to the general health of ptarmigan is stressed by Nordhagen (*op. cit.*). He states that berries have a curative effect (due to the tannic acid content) on birds suffering from coccidiosis, and, if berries are plentiful, the birds are healthier. He tests his hypothesis by correlating the years of a poor berry crop with an ensuing drop in numbers of willow ptarmigan in Norway. A controlled experiment would seem to be still necessary to verify this interesting theory.

Although the annual Newfoundland wild blueberry crop is generally considered to be fairly good, there are indications that it is on the decline. This is particularly true in some sections of the Avalon Peninsula. The Newfoundland Royal Commission on Agriculture (Newfoundland, 1956) reports: "In 1940 the production of blueberries reached its peak. In that year, the crop was estimated at seven and a half million pounds. Since then there has been a material reduction in volume of production as indicated by the export figures. . . . This reduction has been attributed mainly to the work of the Forest Fire Patrol which has been responsible for reducing the extent of burnt-over land upon which blueberries normally grow."

DISCUSSION

The results of this food-habits investigation show that Newfoundland willow ptarmigan are closely associated with a fairly specific ericaceous flora. The common blueberry (*V. angustifolium*) is by far the most important food source for these birds. From this species the leaves, blossoms, fruit, buds, and twigs are eaten, and, depending on the season of the year, some of these plant parts often constitute the entire crop contents. This extensive utilization throughout the year suggests that, providing there is an interspersion of adequate cover, this plant may singularly determine the carrying capacity of a given area for willow ptarmigan.

A plant currently as abundant in many areas of the Avalon Peninsula and exhibiting signs of gaining a selective advantage over *Vaccinium* spp., and especially *V. angustifolium*, is the sheep-laurel (*K. angustifolia*). If this trend continues, there will ensue a gradual deterioration of preferred ptarmigan habitat over much of the Avalon Peninsula. This study has not revealed any utilization of *K. angustifolia* as a food source. It has also been impossible to "trick" our captive birds (35 at the beginning of experimentation), at any age, into taking as much as a bite from this plant. The seed capsules and buds from *K. polifolia*, on the other hand, are occasionally eaten by Newfoundland willow ptarmigan.

Burning, as a method of keeping the Scottish moors in peak production for sheep and grouse, has been practiced for a long time. The Grouse Committee experimented with various methods of burning heather (*Calluna vulgaris*) and came up with recommendations on burning methods on a rotation basis, designed to maintain peak food production with adequate cover for grouse (Lovat, 1911). Heather, according to Wilson and Leslie (*op. cit.*), is the most

TABLE 3.—SUCCESSION, FOLLOWING BARREN FIRES, OF THE TEN MOST ABUNDANT PLANT SPECIES, EXCLUDING LICHENS AND MOSSES, BASED ON 1,000 SAMPLE PLOTS (1 × 0.1 METER) INVENTORIED DURING SUMMER 1956

F = per cent frequency of occurrence. C = per cent ground cover

Elapsed years	0.5–1		2–5		6–9		10–19		20–36		37+	
Number of plots	100		160		160		160		200		220	
Plant Species	F	C	F	C	F	C	F	C	F	C	F	C
Vaccinium angustifolium	99	15	98	36	88	22	89	21	96	13	83	01
Kalmia angustifolia[1]	92	08	67	11	84	22	71	15	89	20	79	18
Cornus canadensis	64	03	92	13	67	06	71	06	86	06	70	03
Vaccinium Vitis-Idaea	71	02	54	04	58	03	72	11	81	10	84	07
Empetrum nigrum	—	—	—	—	03	02	09	02	52	20	62	31
Ledum groenlandicum	11	tr.	24	01	39	03	38	05	59	04	45	03
Maianthemum canadense	51	02	37	02	48	02	57	02	32	01	44	01
Potentilla tridentata	56	03	38	03	30	02	26	01	50	03	56	02
Deschampsia flexuosa	12	04	21	03	12	04	45	06	31	02	40	02
Trientalis borealis[1]	26	01	45	02	21	01	31	01	46	01	48	01

[1] Not a ptarmigan food item.

important food plant for red grouse. The plant occurs only rarely in Newfoundland as an introduced species and has not been found in areas frequented by ptarmigan. The plant is found in Norway, however, and frequently occurs as a food item of the willow ptarmigan there (Olstad and Lid, *op. cit.*).

Burning, as a possible practice in ptarmigan management, is under investigation in Newfoundland. The author is of the opinion that, as many Newfoundland sportsmen contend, the best ptarmigan hunting is generally found in areas that were burned a few years previously. Table 3 shows the results of our preliminary inventory of plant succession, following accidental fires, on barrens usually frequented by ptarmigan. These burns occurred at various times of the year and ranged from a few months to over 37 years in elapsed time since the fires took place.

Although evaluation is not complete, it appears that burning does not destroy much *Kalmia*. This plant has an extensive root system and, following a fire, adventitious stems soon appear and replace those killed. An apparently unfortunate feature pointed out by this survey is the length of time it takes *Empetrum* to reappear. This may be the result of too hot a fire, as most accidental fires occur during tinder-dry conditions. Experimentation with controlled burning may result in a method of controlling the setbacks of this plant, which is an important food source for ptarmigan during the early part of the summer.

Results of this survey show that, for 2 through 5 years following a fire, *V. angustifolium* has an advantage over *K. angustifolia* in both frequency and coverage. After 6 years, however, *Kalmia* exhibits a dominant trend, surpassing *Vaccinium* in coverage in about 20 years. Although this suggests a 5- to 6-year rotation burning program, our knowledge is, at the present time, too meagre to recommend methods for habitat improvement.

The response of some areas following a fire indicate that soil composition and the season in which the burn occurred may be important considerations. There are apparently many factors that impinge upon plant succession on the Avalon Peninsula. Pedological and plant-association investigations will be conducted throughout the ptarmigan range of both Newfoundland and Labrador to find out, among other things, if there is latitudinal change in the interspecific relationships between *K. angustifolia* and *V. angustifolium*.

Although it appears that optimum habitat is disappearing in some sections of the Avalon Peninsula, and that ptarmigan there are not as plentiful as they were formerly reported to have been, there still are areas

on the peninsula that maintain good resident populations.

SUMMARY

Over 300 crops and approximately 500 droppings from Newfoundland willow ptarmigan collected during 1954, 1955, and 1956 were analyzed for this study. Field observations and information acquired from 35 captive ptarmigan are incorporated. Vegetative inventories conducted during two summers, and quantitative comparisons between available food and the food selected by ptarmigan are discussed. From *Vaccinium angustifolium*, the fruit, leaves, buds, blossoms, and small stems are eaten. The year-round and extensive utilization of this plant makes it by far the most important food source for these birds. *Kalmia angustifolia*, a plant not used as food, is apparently increasing, and in some areas frequented by ptarmigan, it is suppressing the desirable *Vaccinium* spp. Investigations of plant succession following fires indicate that in from 2 through 5 years *V. angustifolium* is more abundant than *K. angustifolia*, but after that the trend reverses. Many variables are evidently involved in postfire plant successions.

Ptarmigan food intake during the morning is about the same as required for digestion, with a cessation of feeding around noon. Feeding is resumed at an increased rate during the afternoon. Immature birds, even after attaining full body size, consume more individual food items than do adults. During the fall, berries comprise the bulk of the ingested foods. As winter approaches, there is a change to a more ligneous diet of buds and twigs. During the spring, there is a change back to a more leafy diet; and as summer arrives, the new fruit is eaten as it becomes available.

LITERATURE CITED

BENT, A. C. 1932. Life histories of North American gallinaceous birds. U.S. Natl. Mus., Bulletin 162. 490pp.

CHRISTIANSEN, B. AND A. KRAFFT. 1953. Lirypekyllingenes naering. [The food of willow grouse chicks.] Norges Jeger–og Fisker–Forbunds Tidsskrift, Nr. 4.

GELTING, P. 1937. Studies on the food of the East Greenland ptarmigan. Meddelelser om Grønland, 116(3):114.

GRIMSHAW, P. H. 1911. The insect food of young grouse, based on an examination of crops and gizzards. *In* The grouse in health and disease, pp.88–92. London:Smith, Elder and Co. 512pp.

HAMMOND–SMITH, H. AND R. H. RASTALL. 1911. Grit. *In* The grouse in health and disease, pp.94–99. London:Smith, Elder and Co., 512pp.

HARE, F. K. 1952. The climate of the Island of Newfoundland: a geographical analysis. Geographical Bull., No. 2. 88pp.

HOLMBOE, J. 1924. Hvad lirypen lever av i Norge. [What the willow grouse lives on in Norway.] Bergens Museum Aarbok 1922 and 1923. Naturvidenskapelig rekke, Nr. 5.

KOLDERUP, C. F. 1924. Stenindholdet i kraasen hos norske liryper. [Grits in the gizzards of Norwegian willow grouse.] Bergens Museums Aarbok 1923 and 1924. Naturvidenskapelig rekke, Nr. 4.

KRAFFT, A. 1954. Lirypekyllingenes spisetider. [Mealtimes of willow grouse chicks.] Norges Jeger–og Fisker–Forbunds Tidsskrift, Nr. 6.

LOVAT, LORD. 1911. Moor management. *In* The grouse in health and disease, pp.372–413. London:Smith, Elder and Co. 512pp.

MARTIN, A. C., R. H. GENSCH AND C. P. BROWN. 1946. Alternative methods in upland gamebird food analysis. J. Wildl. Mgmt., 10(1): 8–12.

NEWFOUNDLAND, PROVINCE of. 1956. Report of the Newfoundland Royal Commission on agriculture 1955. D. R. Thistle, Printer to the Queen's Most Excellent Majesty. 391pp.

NORDHAGEN, R. 1928. Rypear og baerar. [Willow grouse and berries.] Bergens Museums Aarbok 1928. Naturvidenskapelig rekke, Nr. 2.

OLSTAD, O. AND J. LID. 1923. Undersøkelser over lirypens naering. [Food of the willow grouse in different localities.] Norsk Jaeger–og Fiskerforenings Tidsskrift, 3:119–138.

ROULEAU, E. 1956. Studies on the vascular flora of the Province of Newfoundland (Canada). Pts. 1, 2, and 3. Contributions de l'Institut Botanique de l'Universite de Montreal, No. 69. 106pp.

STEJNEGER, L. 1884. A new subspecies of willow grouse from Newfoundland. Auk, 1(4):369.

WILSON, E. A. AND A. S. LESLIE. 1911. Observations on the food of grouse, based on an examination of crop contents. *In* The grouse in health and disease, pp. 67–87. London:Smith, Elder and Co., 512pp.

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BEAVER CENSUS METHODS IN THE ROCKY MOUNTAIN REGION[1]

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This paper is an evaluation of numerous beaver-census techniques as they apply to the Rocky Mountain region. In designing plans for management of the beaver (*Castor canadensis*), primary consideration must be given to enumeration and appraisal of extensive populations. Reports on surveys of this nature (Atwater, 1940; Tappe, 1942; Bradt, 1947; Swank and Glover, 1948; Fuller, 1953; and Knudsen, 1951, 1954), varying widely in approach and results, have been relatively frequent. In these studies, the census techniques mentioned have dealt almost exclusively with the use of lodges, dams, slides, food caches, and scent mounds as indices of beaver numbers. Verification of the accuracy of such population measurements was a necessary requisite for sound management plans in mountain terrain.

In hundreds of publications concerned with the beaver, over 30 referred specifically to some form of beaver census (Yeager and Hay, 1955). The lodge was the most universally used index, many authors considering it synonymous with the beaver colony. Estimations of colony numbers, based on beaver "sign," were next in frequency of use. And mentioned as a part of some census methods was the winter food cache, usually considered certain evidence of the presence of a beaver family (Hammond, 1943; Blomquist, 1951; Townsend and Newby, 1955). In all of these studies, the estimated number of animals in individual colonies was based upon one or more of the following: size of the food pile, width of incisors on cut wood, measurement of hind footprints, size of the lodge, number of lodges, and size of "smoke-holes" in the snow on the roofs of lodges.

Location and Description of Areas

Field studies were conducted in three counties in Colorado, on study areas considered typical of beaver range in the central Rocky Mountain region.

Jackson County.—Investigations in Jackson County centered on the North Fork of the North Platte River, within a rectangular tract 2½ miles long and 1 mile wide. The four locations here involved one stream and three seepage areas at elevations between 8,600 and 9,500 feet. Floodplains varied from channel width to 515 feet, and stream gradients at the colony sites varied from 2 to 7 per cent. The main beaver foods were aspen (*Populus tremuloides*), willows (*Salix* spp.) and pond lilies (*Nuphar* spp.).

Grand County.—Lost Creek, a tributary of the Williams Fork River, constituted the second area, 2½ miles in length. The stream elevation was 8,980 to 9,200 feet; its floodplain varied from channel width to more than 240 feet; and the gradient at colony site ranged from 1.0 to 2.5 per cent. The source of beaver food consisted primarily of willow.

Saguache County.—Nutras Creek, a tributary of Cochetopa Creek in south-central Colorado, was studied critically along 1½ miles of stream. Elevation ranged from 10,000 to 10,800 feet. The floodplain averaged 40 feet in width, but at one point extended to 360 feet. The mean stream gradient was 5 per cent. Willows constituted the principal beaver food.

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On these three areas a total of 13 colonies were studied intensively; 6 in Jackson County, 4 in Grand County, and 3 in Saguache County. The Jackson and Saguache County areas were on glacial till, their topography shaped in many places by lateral and terminal moraines. The area in Grand County was a valley formed in extensive deposits of alluvium.

Localities affording undisturbed beaver populations were selected in Jackson and Saguache counties. The Grand County area had previously been trapped to extirpation during the fall of 1954 and the winter and spring of 1955 by Colorado Game and Fish Department personnel. Detailed records of the location and number of animals trapped were available.

METHODS

Time.—Field work covered two summer and early-fall periods: June to October 1954, and June to November 1955.

Census Methods.—Live-trapping, using the Hancock trap, was conducted almost continuously and with equal effort during both summers on the Jackson County sites. Prior to release after capture, each animal was ear-tagged for later identification. Dead-trapping was carried out intensively in the fall of 1955 in Jackson and Saguache counties to insure exact enumeration of all beavers present. Pertinent data, such as age and sex, were recorded for all animals handled in each operation (Table 1).

Observations of the Jackson County colonies were made throughout the first summer, each observation averaging 121 minutes in length. Several vantage points suitable for observational purposes were located downwind near each population center, and were situated to permit unimpaired visibility.

Pond draining and excavating operations were undertaken in attempts to count resident beavers. Over 30 men participated in some cases. Smoke cartridges were used in further efforts to drive beavers from their shelters. After the pond level had been lowered, revealing lodge entrances, a small hole was made in the structure and the smoking apparatus inserted. All ponds so treated were on other than the three main study localities.

Two aerial censuses of each location were taken during late October and early November 1955. A 2-place Piper Cub plane, flying at altitudes varying from 50 to 200 feet above the ground and at approximately 60 miles per hour, was used for this purpose.

Identification Techniques.—To determine territorial boundaries, ranging habits, and

TABLE 1.—NUMBER, AGE, AND SEX COMPOSITION IN BEAVER COLONIES, COLORADO

Area	Colony Number	Composition							Total
		Adults		Yearlings		Kits		Misc.	
		M	F	M	F	M	F		
NORTH PLATTE RIVER	1	1	1	1	2	1	4	–	10
	2	2	3	1	–	–	–	1 adult	7
	3	1	1	1	1	–	4	–	8
	4	2	–	–	–	–	1	–	3
	5	Composition Unknown[1]							11
	6	3	3	–	–	–	–	1 kit	7
LOST CREEK	1	1	1	–	–	2	–	–	4
	2	3	3	1	–	–	–	–	7
	3	2	3	1	–	–	–	–	6
	4	1	1	–	–	–	–	–	2
NUTRAS CREEK	1	1	1	–	1	–	–	–	3
	2	2	1	–	1	–	1	–	5
	3	2	2	2	1	–	1	1[2]	9

[1] Trapping by state trappers who kept accurate records of the number of animals; sex and age not recorded.

[2] After all beavers were thought to have been taken in each area, traps were left set for five additional nights. In this case one trap was set off during the interval, accounting for the additional animal.

intercolonial movements, it was necessary to distinguish between the individual beavers in certain colonies.

Spraying the pelage with bright enamel paints proved to be unsuccessful. After approximately two days, the animals' constant combing habits removed virtually all of the color. Painting half of the dorsal surface of the tail was more satisfactory, with identification possible for as long as one month. The crepuscular and nocturnal habits of beavers prompted the use of luminous paints. Again only the tail retained the color material. Although it was not possible to see the painted tail "glow," the paint seemed brighter than the enamel in late-evening light.

Clipping the fur in definite patterns also proved worthwhile. Wide lateral strips, clipped as closely as possible, were readily seen and lasted longer than any of the other methods.

A 3 per cent solution of hydrogen peroxide was used in an attempt to bleach portions of the pelage. Due to the oily nature of the fur, the relatively weak peroxide solution had no effect.

Ear-tagging was a simple and easy means of identifying trapped animals at later dates. Size 3 monel-metal fish tags, roughly ½ inch long, were used.

FINDINGS AND DISCUSSION

Delimitation of Colony Area.—Colony locations were of two types: "isolated" and "multi-colony." The first type occurred on small tributaries or seepages, where the colony's territory was easily delimited by natural land features and a definite periphery of beaver activities, e.g., cuttings, trails, and scent mounds. The second type consisted of areas where generations of beavers had so populated the available habitat that colony isolation no longer existed. Here, the delineation of boundaries was difficult and required intensive observation and live-trapping. Although the family unit in these cases occupied a definite section of the stream, there appeared to be no "property line" involved, regardless of the proximity of other colonies. Instead, there seemed to be a certain pond, or ponds, wherein one colony's territory ended and the adjacent one's began. The dams supporting these ponds were kept in good repair through the co-operative efforts of both colonies. This fact was substantiated by the origin and position of food paths surrounding such neutral waters and by actual observation of the animals using the routes and ponds.

Scent mounds occurred in noticeably concentrated patterns around inhabited sites, and these structures appear to indicate some relationship to territoriality. No scent mounds were found between inhabited areas. The number of scent mounds per colony showed wide variations (Table 2)—one colony of three animals built 29 mounds, and another of three beavers built only two. Such variation excludes scent mounds from further consideration for census purposes. Moreover, counting scent mounds, particularly in willow swamps, is exceedingly difficult and time consuming. For strictly "trend" surveys, annual scent-station counts, in conjunction with lodge and slide counts, are being used in Oregon (Ore. State Game Comm., 1957).

Correlation between Beaver Numbers and Structures.—The location of colonial boundaries served to identify beaver constructions with the appropriate colony. Such knowledge forms the basis for correlating a colony's population with the number of their observable constructions. No significant statistical relationship existed between the number of beavers and the size of the main lodge. There is, of course, a definite physical limitation in the size of a lodge and the number of animals that it can house, but no visual population estimate can be based upon this fact. Large lodges did not always contain proportionally larger families (Table 2).

No analysis was attempted between the number of lodges per colony and the size of the colony. To associate more than one lodge with a particular colony is often impossible without an intensive ground study, thus rendering such practices impractical from a census standpoint.

TABLE 2.—NUMBER OF BEAVERS PER COLONY, SIZE OF MAIN LODGE, AND NUMBER OF OBSERVABLE CONSTRUCTIONS, COLORADO

Area	Colony Number	Number of Beavers[1]	Size of Main Lodge[2]	Number of Active Lodges[3]	Number of Food Caches[4]	Number of Scent Mounds
NORTH PLATTE	1	10	857.6	2	1	6
	2	7	2618.0	1	1	3
	3	8	390.0	2	1	14
	4	3	354.3	1	1	2
	5	11	906.7	1	1	11
	6	7	2436.0	3	1	6
LOST CREEK	1	4	851.0	1	1	0[5]
	2	7	472.5	1	1	0
	3	6	928.0	1	1	0
	4	2	1398.6	1	1	0
NUTRAS CREEK	1	3	249.9	3	1	29
	2	5	252.0	3	1	12
	3	9	1143.8	3	1	34

[1] From dead-trapping, verified observations, and tagging returns. [2] Maximum length × width × height in feet, expressed as a multiple. [3] Lodges known to be occupied during the summer. [4] From ground observations. [5] Data not available on these colonies.

During the summer months, beavers were found to inhabit various dwellings other than their main overwintering lodge. These consisted of "summer" lodges, small lodge-like huts, and bank shelters. One colony may keep in good repair as many as three different lodges (Fig. 1). During the fall, the individuals comprising the colonial group vacate these structures and build a common food cache and utilize a single lodge for winter quarters. This communal habit in wintering beaver populations can be accounted for, perhaps, by the following reasoning: It would indeed be improbable that the beaver, a pronounced aquatic mammal, could survive the intense winters in the high mountains without relatively deep water, a stored food supply, and the added thermal value inherent in the immediate proximity of a number of warm-blooded animals. Gregariousness, therefore, serves as a protective function in groups of related beavers.

In Canada, Symington and Ruttan (1956) concur that a single beaver family may require two or three lodges due to an extensive feeding range. And in Russia, Semyonoff (1953) noted that beavers show ". . . a tendency to form colonies of related families."

Differentiation between temporary "summer" lodges and the main lodge is virtually impossible from the air without the identifying food cache. The lodge, although the most universally used index for censusing beavers, is evidently not synonymous with the colony.

No analysis was necessary between the number of food caches and colonies involved, since complete correlation was noted in the data obtained (Table 2).

The use of slides or food paths and the presence of dams and ponds were not considered as census indices because of their obvious dependence upon topographical conditions and proximity of food, rather than number of animals.

Correlation between Beaver Numbers and Food Sources.—Colonies subsisting mainly on aspen contained significantly larger numbers of beavers than those living predominantly in willow habitats. The average of five colonies subsisting on aspen was 7.8 animals; seven willow-supported colonies averaged 5.1 beavers. In the colonies having young, those on aspen averaged 1.5 yearlings and 2.5 kits, while those on willow averaged 1.1 yearlings and 0.6 kit. Although colonies utilizing aspen averaged 2.6 more animals and 2.1 more young, I consider further investigations necessary for the development of values fully reliable for census purposes. In New Mexico, Huey (1956) found that pregnant females averaged 4.5 embryos on aspen habitats, 2.7 on cotton-

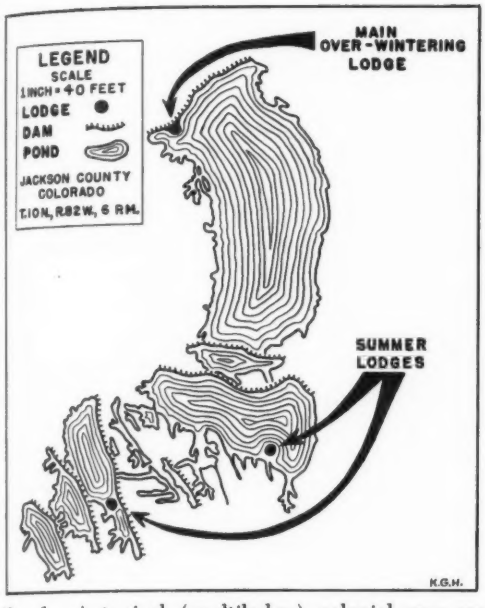

FIG. 1. A typical (multilodge) colonial area on Goose Creek, Jackson County, Colorado. A colony of seven beavers occupied and maintained three separate lodges, but chose only one for overwintering purposes. Such dwelling practices were common for beaver colonies in mountainous terrain.

wood types, and 2.0 on willow types. Somewhat similar findings in Colorado were reported by Yeager and Rutherford (1957).

The number of beavers per colony, in relation to stream gradient and width of floodplain at the site, was plotted to determine whether correlations were apparent. It was evident that no significant relationship existed. Thus, the role of environmental features of a physical nature in censusing beaver populations seems to have no utility, aside from their possible effect on the type and amount of food made available.

Bank Dens.—Bank lodges, in the sense of primary colony habitation structures, were never encountered on any of the areas studied or incidentally visited during the course of investigation. Although such structures possibly occur, they are not considered an important source of error in censusing beavers at high altitudes in the mountain terrain of the Rocky Mountain region.

On large streams at lower elevations, however, aerial flights revealed the frequent occurrence of food caches. Bank dens on such streams appear to be important overwintering structures. Probably the availability of water deep enough above bank entrances to safeguard against blockage by ice and the difficulty of building lodges where there are extreme water-level fluctuations and strong currents accounted for this difference.

The only type of bank abodes present on the areas under consideration were burrows, usually short and fairly well concealed. These dwellings were present in varying numbers at all locations, and seem to represent only temporary summer shelter for one or a very few animals.

Age and Sex Ratios.—Dead-trapping records (Table 1) revealed that 2 to 11 beavers constituted the colonies studied in this investigation. The data, taken during October and November and extending through April on the Lost Creek colonies, indicate sex and age ratios and the number of overwintering beavers at each site. It is difficult to account for the atypical composition of colonies containing more than two adults and their offspring, as exemplified by Bradt's (*op. cit.*) findings. Despite precautions, errors in trapping are possible, but their consistent occurrence is improbable, especially in isolated colonies where traps remained set and close checks were made from October through April. The commual living habits of related beavers during the winter may explain such atypical composition at high altitudes.

The sex of all animals handled was 31 males and 37 females, or a ratio of 83 males: 100 females. The average number of beavers per colony was 6.3 ± 1.3 (95 per cent confidence limits) with a standard error of 0.75. Semyonoff (1951), while engaged in live-trapping operations in the Archangel Province in Russia, found that the average beaver family consisted of 6.2 animals.

The Best Season for Censusing.—In the fall, beaver activities in the study areas became more intense and localized; repairs on the winter quarters were begun by mid-September. By October, food caches had been completed, summer lodges vacated, and the colonial group established in their winter lodge. Deciduous trees had lost their

leaves, and many of the ponds had frozen over prior to the first of November. Snow and high winds after this date made aerial censusing considerably more difficult than in October. Early fall, i.e., late September through October, is obviously the most advantageous time for census operations.

A Practical Beaver-census Method.—The technique that proved to be rapid, reliable, and relatively economical involved an aerial coverage with suitable craft. The count of food caches from the air was exactly the same as that recorded on the ground. I believe that such enumeration constitutes the most reliable and practical method suitable for application over large areas.

The food cache is always constructed in the water, thus affording a contrast vitally important in identification. Lodges, the count of which has already been mentioned as an unreliable index, are in addition difficult to locate unless they are also surrounded by water. Of the 23 lodges on the study areas, 10 were located along shorelines and, in every case, were difficult to distinguish, aloft, from the surrounding terrain. Only the presence of the food cache permitted positive recognition.

An average of 5 hours of ground observations was required before the highest count was recorded on any colony. Moreover, this count was not in all cases the total population that was later revealed by trapping records. The error was usually concerned with the kits, which appeared for only short, infrequent periods. Despite the unreliability of this method as a census endeavor, it enabled the writer to observe intracolony movements and interspecific relationships and aided in the establishment of colony boundaries.

Pond draining and excavation were conducted at six well-delimited colony sites. Out of the six colonies, only two kits were captured and only two adults were observed leaving the lodges. The use of smoke bombs to drive beavers from their shelters was tried on two colonies. The method proved to be completely futile.

Live-trapping was too slow and unreliable to serve as a practical census method, although it aided in subsequent restudy of animals and made possible the recording of movements, and thus the home affinities, of various beaver groups. Later, dead-trapping of colony inhabitants revealed that not all of the residents, especially kits, had been live-trapped and marked. Dead-traping was found to be more accurate and expedient than live-trapping, and when conducted in the late fall revealed the true colony composition. In either case it is difficult to account for every animal.

The wide distribution of beavers in mountain terrain decrees that a census method be extensive in application, preferably via aerial coverage. Application, however, is dependent upon investigations intensive enough to yield the necessary basic information. To this end, dead-trapping is essential in obtaining reliable index values for average winter-colony numbers. Sound research findings as to altitudinal and food variations should be incorporated to refine index values for these varying conditions. With such predetermined values, the number of food caches in a given area may be counted, either on foot or from the air; and, when multiplied by the index figure, a reliable and practical census of the resident beavers is obtained. Barring a radical change in Colorado's beaver population, I feel such census findings will meet all requirements for practical management purposes.

The application of this census method is necessarily restricted to mountain areas, since beavers on the plains frequently do not build food caches. In addition, downstream populations are subjected more to unstabilizing pressures than are mountain-situated beavers. Such factors as damage-control trapping, the sudden elimination of habitat through logging, clearing, or road-building, and the effects of pollution, siltation, and overuse by man and livestock, render inapplicable techniques based on population constants.

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SUMMARY

Thirteen beaver colonies, in three localities in Colorado, were investigated over two summer and fall periods. Areas affording typical beaver habitats, with populations living under varied food and environmental conditions, were selected for census by ten different procedures.

Live-trapping was found to be unreliable as an intensive census method. Dead-trapping was used in determining the average number of beavers per wintering colony. Observations, pond draining, and dislodging with smoke cartridges proved to be grossly inadequate for census purposes. Dams, scent mounds, size of the main lodge, and the number of lodges were likewise invalid as population indices. The lodge was not synonymous with the colony, despite popular supposition. One colony may keep in good repair through the summer at least three different lodges. On none of the areas investigated were bank dens used by beavers as wintering dwellings.

Aerial coverage of drainages, using the food cache as an index, was found to be both accurate and practical. In each case there was one food cache per colony and the cache, always surrounded by water, could be easily recognized.

Physical features of the environment seemed to have no apparent bearing on the censusing of beaver populations, aside from their effect on the type and quantity of beaver food. Colonies subsisting mainly on aspen were found to contain a significantly larger number of individuals (7.8) than colonies subsisting predominantly on willow (5.1). Extirpation via dead-trapping of all colonies studied indicated an average of 6.3 ± 1.3 beavers per colony. The sex ratio was 83 males : 100 females.

A reliable and practical census of the beaver populations in mountain terrain, by drainages or other units, may be obtained by counting, either on foot or from the air, the number of food caches in a given area in late September or October and multiplying by the average number of beavers per winter colony.

LITERATURE CITED

ATWATER, M. M. 1940. South Fork (Montana) beaver survey: 1939. J. Wildl. Mgmt., 4(1): 100–103.

BLOMQUIST, W. 1951. Censusing techniques. N. Dakota Outdoors, 13(10):6–8.

BRADT, G. W. 1947. Michigan beaver management. Mich. Dept. Cons., Game Div. 56pp.

FULLER, W. A. 1953. Aerial surveys for beaver in the Mackenzie District, Northwest Territories. Trans. N. Amer. Wildl. Conf., 18: 329–335.

HAMMOND, M. C. 1943. Beaver in Lower Souris Refuge. J. Wildl. Mgmt., 7(3):316–321.

HUEY, W. S. 1956. New Mexico beaver management. New Mexico Dept. Game and Fish, Bull. No. 4. 49pp.

KNUDSEN, G. J. 1951. Annual census and trapper harvest. Fed. Aid Quart. Prog. Rept., Wisconsin, Project W-15-R-7, Job I-C, pp. 80–81.

———. 1954. Annual beaver census. Fed. Aid Quart. Prog. Rept., Wisconsin, Project W-15-R-7, Phase B, Job I-A, pp. 113–120.

OREGON STATE GAME COMMISSION. 1957. Fur bearers. Annual report, Game Div. 176pp.

SEMYONOFF, B. T. 1951. The river beaver in Archangel Province. Translations of Russian Game Reports [Canadian Wildl. Serv., Ottawa, Canada, 1957, 109pp.], 1:5–45.

———. 1953. Beaver biology in winter in Archangel Province. Translations of Russian Game Reports [Canadian Wildl. Serv., Ottawa, Canada, 1957, 109pp.], 1:71–92.

SWANK, W. G. AND F. A. GLOVER. 1948. Beaver censusing by airplane. J. Wildl. Mgmt., 12 (2):214.

SYMINGTON, D. F. AND R. A. RUTTAN. 1956. Beaver in Saskatchewan. Sask. Dept. Nat. Res., Cons. Bull. No. 1. 17pp.

TAPPE, D. T. 1942. The status of beavers in California. Calif. Dept. Nat. Res., Div. Fish and Game, Game Bull. No. 3, 59pp.

TOWNSEND, J. E. AND F. E. NEWBY. 1955. Montana beaver management. Proc. Western Assoc. Game and Fish Comm., 35:269–278.

YEAGER, L. E. AND K. G. HAY. 1955. A contribution toward a bibliography on the beaver.

Colo. Game and Fish Dept., Tech. Bull. No. 1. 103pp.

YEAGER, L. E. AND W. H. RUTHERFORD. 1957. An ecological basis for beaver management in the Rocky Mountain region. Trans. N. Amer. Wildl. Conf., 22:269–299.

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DESIGN TESTS FOR MOURNING DOVE CALL-COUNT SAMPLING IN SEVEN SOUTHEASTERN STATES

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This paper reports on a test of the efficiency of contemporary mourning dove call counts in seven southeastern states, with particular reference to tests of a sampling design that will yield more reliable data.

The call count has been used as an index to the population of calling mourning doves (*Zenaidura macroura*) since 1951. Fundamental research on this technique was conducted from 1950 to 1956 as a part of the Cooperative Dove Study. Initial research on the call index was conducted by a number of workers in different parts of the United States (Foote and Peters, 1952; Wagner, 1952; McGowan, 1952, 1953; Kerley, 1952; Duvall and Robbins, 1952; Peters, 1952; Davey, 1953; and Southeastern Association of Game and Fish Commissioners, 1957). Extensive data gathered by co-operators in recent years from 600–700 routes in 44 states annually have been used for management information. Analysis of call-count data from the original management routes by life zones, biotic provinces, soils, and political boundaries has suggested some fundamental relations between populations and ecology. More conclusive evidence of these relations, however, has awaited collection of call-count population data from a statistically appropriate sampling.

Although some of the original call-count routes were selected on an ecological basis, at least in the Southeast, many of the routes may have been chosen because they were known to sustain moderate to good dove populations or because they were convenient to an observer. The degree of randomness in selection and of representativeness of area and population of the original management routes was unknown. Data from these routes have been used chiefly to denote changes in the population of calling doves on the same routes from year to year. Attempts have been made to weight calling populations by land areas for hunting-regulation information and for design of a nation-wide nestling-banding program, using data from original management routes, because these were the best data available on dove populations.

To permit area-to-area comparisons and proper weighting of call-count data from geographic areas, the population data so used either should be obtained under principles of randomization, or the sampling biases related to nonrandomness should be estimated and used as correction factors. A test to compare data resulting from random sampling with that obtained from the present system of sampling has been of high priority in the over-all dove-management program (Foote, 1953, 1957). This report summarizes results from this test.

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METHODS

The seven southeastern states of Alabama, Georgia, Kentucky, Mississippi, North Carolina, South Carolina, and Tennessee comprise a dove-productive land area of approximately 313,800 square miles. In this area between 140 and 150 dove call-count routes have been censused annually since 1951 (Southeastern Association, *op. cit.*).

The call-count technique is limited in application to sections of the dove range traversed by roads because it consists of 20 systematic auditory plots with about ⅝-mile radii, at 1-mile intervals, on which all doves heard are counted. It is limited to nonurban areas where noise does not interfere with one's hearing calling birds, and is best adapted to lightly traveled roads. Its adaptability in areas having high dove-calling populations is unknown, but it is very efficient in areas having low calling populations. Weather, time of the morning, season, and other factors that influence the counts are generally understood, and the nation-wide counts have been rigidly standardized to eliminate much of this innate variation (Southeastern Association, *ibid.*). Data on sample size for known precision from the original call-count routes have been compiled and were used in determining the sample size desirable for this test, in relation to man power available. A trained corps of observers, with a background of several years' experience, was available for conducting the test in the 7-state area.

Throughout this paper, "original management" routes are regularly censused routes on which mourning doves have been counted for several years, while "random" routes are those especially selected for this study.

Sampling employed for the random test was stratified random sampling (Table 1). Stratification by states was based upon average calling populations heard on the 142 routes that were censused from 1954 to 1956, inclusive.

A map of the 7-state area was gridded into squares (cells) 20 miles on a side, each enclosing 400 square miles. A total of 785 sampling cells thus constituted the frame,

TABLE 1.—APPORTIONMENT OF SAMPLING, RANDOM CALL COUNT, 1957

State	No. Routes 1956	Mean Doves 1954–1956	Prod. Land Area Sq. Mi. (100 s)	Index	Per Cent of Total	No. Random Routes	No. Cells
N.C.	18	23.7	442	104754	13.3	21	119
S.C.	22	32.9	306	100674	12.8	20	76
Ga.	18	18.7	585	109395	13.9	22	145
Ala.	20	28.2	510	143820	18.2	28	129
Ky.	17	25.2	401	101052	12.8	20	96
Miss.	16	23.3	474	110442	14.0	22	117
Tenn.	31	28.4	420	119280	15.1	24	103
Totals	142		3,138	789417	100.1	157	785

enclosing 314,000 square miles, which approximates the estimated 313,800 square miles of dove habitat in these states. Major metropolitan areas were omitted from the frame; also omitted were areas containing major bodies of water. The periphery of the 7-state area was corrected by omitting approximately one-half the incomplete grids on the boundary.

A one-in-five sampling yielded 157 cells and provided approximately the same number of random routes as there were regular annually censused call-count routes within the test area. County road maps enclosing the area in each randomly selected cell were obtained. The periphery of each cell was divided into 80 1-mile intervals, starting at the northeastern corner and proceeding clockwise. Twenty lineal miles then were mapped from that point which had an appropriate road closest to the 1-mile interval selected at random, proceeding generally toward the center of the cell and staying within the cell boundaries. Selected roads were those that appeared (by the map) to be traversable. Intermittent roads, ferries, or major unbridged streams were avoided. Main highways were not included, except for short distances when it was not possible to select a more appropriate route. Urban areas, railroads, airfields, and roads adjacent to major highways were avoided, and the route did not "double back" upon itself on roads closer than 1 mile. Acute-angle turns were avoided to prevent duplication of auditory plots at successive stations.

Slight adjustments of less than 2 miles occasionally were made to provide a readily recognizable starting point for the route. The starting point was determined to be that end of the route most easily reached from a main highway and population center. All routes were selected by a mapper unfamiliar with the area. When confronted with alternatives within the preceding limitations, roads were selected at random.

To prevent introduction of observer differences, routes were assigned in pairs of original management and random routes when this was possible, and observers were instructed as to which route to census first in order to alternate the routes. Observers were asked to drive over the random route once before conducting the census to become familiar with the route. The census procedure was exactly the same for both original management and random routes and was that which has been employed nationally since 1951 (Southeastern Association, *ibid.*).

Data were analyzed using standard statistical procedures described by Cochran (1953) and Snedecor (1956). For purposes of comparison with the random sample, the original management sample was considered to be a second stratified random sample.

Means of the two samples were computed as follows (Cochran, *op cit.*):

$$\bar{y}_h = \frac{\sum_{i=1}^{N_a} y_{hi}}{n_h} \quad \text{sample mean of stratum } h$$

$$\text{and } \bar{y}_{st} = \frac{\sum_{n=1}^{L} N_h \bar{y}_h}{N},$$

estimated population mean per unit.

Estimated variances of the sample mean, $\bar{y}_{st}$, were determined as follows:

$$v_{\bar{y}_{st}} = \frac{1}{N^2} \sum_{n=1}^{L} N_h(N_h - n_h)\frac{s_h^2}{n_h}$$

$$\text{where } s_h^2 = \frac{1}{(n_h - 1)} \sum_{i=1}^{n_h} (y_{hi} - \bar{y}_h)^2.$$

The approximate precision that would have resulted from ecological stratification was compared with that for state strata after dividing the data into ecological boundaries previously used in dove research in this area (Southeastern Association, *op. cit.*).

An estimate of the variance had sampling been completely random (no stratification) is given by

$$v_{ran} = \frac{N-n}{nN}\left[\sum W_h s_h^2 - \sum \frac{W_h s_h^2}{n_h} + \sum \frac{W_h^2 s_h^2}{n_h} + \sum W_h \bar{y}_h^2 - \left(\sum W_h \bar{y}_h\right)^2\right]$$

This estimate is also compared with the precision of the stratified random sample actually selected.

TABLE 2.—COMPARISON OF STRATIFIED MEANS AND VARIANCES OF DOVES *Heard* AND DOVES *Seen* ON RANDOM AND ORIGINAL MANAGEMENT ROUTES IN SEVEN SOUTHEASTERN STATES, 1957

	Number	Doves Heard		Doves Seen	
		Stratified Mean	Variance (st)	Stratified Mean	Variance (st)
Random routes	150	25.08	1.667	23.29	3.669
Management routes	141	28.50	1.667	24.94	2.911
t value, difference, means			1.868		0.643
$t_{.05}$			1.97		1.97

RESULTS AND ANALYSES

Comparison of Random and Original Management Routes

A total of 150 random and 141 original management routes were censused under the standardized technique in the 7-state area between May 20 and June 10, 1957. In only a few instances were changes necessary on parts of the random routes because of impassable roads. Seven of the random routes were not censused.

There was only a slight tendency for observers to census the original management routes first; the difference between mean day of census of the random and original management samples was not significant.

On the average, more doves were *seen*, as well as *heard*, on the original management routes; variances in the doves *heard* were the same numerically for both samples, indicating a slightly higher relative variability in the random sample (Table 2).

Variances of doves *seen* were greater than those of doves *heard*, confirming conclusions previously made from the original management data alone (Southeastern Association, *ibid.*). The variance of doves *seen* was greater in the random sample than in the original management sample.

Differences between doves *heard* on random and original management samples fell just short of significance by t test at the 5 per cent level (significant at 6.1 per cent), suggesting that the original management sampling may be positively biased in selection of higher dove population areas in this region.

Consideration of data from the state subsamples (Table 3) indicates only one "reversal." In only one state stratum (North Carolina) was the population *heard* on random routes higher than that on original management routes; only two strata (Georgia and South Carolina) had higher mean dove populations *seen* on random routes than on original management routes. A sign test (Snedecor, *op. cit.*) also indicated a difference just short of the 5 per cent significance level between doves *heard* on random and on original management routes in the seven states.

TABLE 3.—COMPARISON OF STATE SUBSAMPLES, DOVES *Heard* AND *Seen*, SEVEN SOUTHEASTERN STATES, 1957

State	Number			Doves Heard				Doves Seen			
	Cells	Random Routes	Mgmt. Routes	Random Mean	Random s	Management Mean	Management s	Random Mean	Random s	Management Mean	Management s
Ala.	129	27	20	21.1	15.2	30.2	15.3	18.2	14.2	24.6	26.3
Ga.	145	21	17	22.0	15.3	22.4	13.3	18.9	34.1	12.8	8.9
Ky.	96	17	16	23.3	16.1	28.1	15.3	28.9	28.9	33.2	23.6
Miss.	117	21	16	26.0	13.8	27.4	15.4	28.8	23.6	30.8	28.6
N.C.	119	21	18	24.4	20.2	23.6	14.6	20.8	17.7	24.8	18.6
S.C.	76	19	23	26.3	19.7	34.9	32.0	23.1	29.5	18.1	23.6
Tenn.	103	24	31	34.9	22.8	37.5	17.0	27.4	19.2	33.3	15.6
Stratified averages or totals	785	150	141	25.08		28.49		23.29		24.94	

TABLE 4.—COMPARISON OF DIFFERENT SAMPLING DESIGNS; DOVES *Heard* AND DOVES *Seen* ON RANDOM CALL-COUNT ROUTES, SEVEN SOUTHEASTERN STATES, 1957

Type of Sampling	No. of Strata	Doves Heard		Doves Seen	
		Variance	*F* Test	Variance	*F* Test
Stratified random state strata	7	1.667	1.731	3.673	.0996
Random sampling	1	1.702	——	3.265	——
Stratified random ecological strata	9	1.391	3.067**	2.104	5.30**

** Differences among strata means significant at 99 per cent level.

The mean biases of state strata of doves heard varied from –0.8 to +9.1 doves. In one state, Alabama, the mean bias was significantly different from zero.

Random Route Sampling Design

Table 4 shows that some very slight improvement resulted from stratification of the sampling by state strata, when compared with complete randomization. The table indicates that precision was lost in the estimate for doves *seen* by the state stratification employed. However, this stratification was based upon mean doves *heard*, not upon previous data of doves *seen*, so improvement from stratification in estimates of variance of doves *seen* was not anticipated.

Better precision (17 per cent improvement) of the estimate of doves heard probably would have been obtained through stratification of the sampling by major ecological divisions. There are some rather clear differences in mean populations of doves, both *heard* and *seen*, that confirm information from nation-wide original management routes when these are divided into life zones or into biotic provinces (Southeastern Association, *op. cit.*).

Table 4 also includes results from variance analysis of data from random routes and shows highly significant differences among strata means of doves both *seen* and *heard* when the data were divided into ecological strata. Means of state strata were not significantly different in either the *heard* or *seen* groups from the variance analysis.

Table 5 gives means, number of routes, and cells into which the data fell when divided into ecological strata. On low-population routes, the number of doves *seen* averages less than the number *heard*, while on high-population areas the reverse is true. The general relation between means of doves *heard* and means of doves *seen* by ecological areas is evident. Nation-wide call-count data from original management routes show a similar relation (Southeastern Association, *ibid.*).

DISCUSSION

As compared to randomly selected routes, the presently employed dove call-count

TABLE 5.—RANDOM CALL-COUNT RESULTS BY ECOLOGICAL STRATA

Stratum	Number Cells	Number Routes	Mean Doves	
			Heard	Seen
Lower Coastal Plain	70	11	12.8	7.2
Upper Coastal Plain	273	47	26.2	19.0
Piedmont	123	28	23.3	26.3
Appalachian valleys and ridges	54	12	26.8	20.3
Blue Ridge Mountains	41	6	8.0	0.7
Allegheny–Cumberland Plateau	52	9	6.4	2.7
Hills, terraces, Miss. alluvial bottoms	74	18	38.4	41.9
Highland Rim, W. Ky. Shale and Sandstone	67	13	34.4	39.0
Bluegrass and Nashville Basin	31	6	38.8	26.8
Weighted means or totals	785	150	24.68	21.32

routes in seven of the Southeastern States are positively biased and, therefore, higher-than-average dove population areas are being sampled. The original management routes in these seven states may have been selected purposefully and are not representative of the dove population in this area. The differences between the random sample and the original management sample were not great, which should be reassuring to the administrator considering these data for hunting regulations.

Unless it can be shown that the bias in the mean is constant from year to year and from area to area, detection of population change from original management-sample data has an error potential. Because the bias in original management-route data tends to be positive over the different population densities in the state strata, it might be inferred that the original route bias would also be positive over year-to-year changes in density. This could be tested only by continuing to sample both random and original management routes for several years to determine if both sets of population data fluctuate synchronously.

While the management-route data reflect calling-population changes *on those routes from year to year*, these data cannot be shown to reflect actual population change from year to year within the 7-state sampling area because of the relatively large bias and because the year-to-year harmony between original management-route data and those from a random sampling is unknown. In the state strata, the biases, while generally positive, differ considerably in magnitude, so the original management data cannot be used for area-to-area comparison with the accuracy necessary for management.

Comparisons of variance of sampling by state and by ecological-zone stratification indicate that the latter is approximately 17 per cent more efficient than the former. This confirms information from analyses of 1953 and 1954 call-count data (Southeastern Association, *ibid.*). Use of the data for population-weight factors for banding analyses will be more precise if the data are stratified first by ecological zones, then by states or areas of interest. This also applies to the original management data.

CONCLUSIONS

1) The presently employed dove call-count routes in seven of the Southeastern States are positively biased, and higher than average dove population areas are being sampled by the original management routes.

2) The difference between mean numbers of doves heard calling on original management routes and on randomly selected routes was small, but approached significance at the 95 per cent probability level. Data from the original management routes have been used since about 1951 in planning hunting regulations. It should be reassuring to the wildlife administrator that differences between the means of the two sets of routes were not of greater magnitude than they were.

3) The nation-wide call-count sampling should be revised so that censusing is conducted on routes selected by a statistically appropriate system.

4) Selection of routes should be on the basis of stratified random sampling by ecological zones. For administrative purposes, data from ecological-zone strata can be combined by states or by other political groupings to relate areas of harvest and production for hunting-regulation purposes. To establish banding quotas or for other management or research programs, weighting by ecological zones is more appropriate than weighting by any other presently known system.

The number of routes necessary for sampling by ecological zones can be approximated from the call-count route data gathered from 1951 to 1957 and from the random data gathered in this study. The sample size required will depend upon the expected variance in each ecological zone, and on the precision required from the estimates within each area of interest. Use of the finite population-correction factors is recommended if the sampling density exceeds five per cent of the cells.

5) Revision of the nation-wide sampling should be undertaken as soon as possible.

To permit use of the call-count data for management purposes, especially for hunting regulations, in conjunction with randomization of the sampling, there are two alternatives. (a) A completely new randomly selected series of routes can be designed and both random and original management sets of routes censused the first year. The original routes would be dropped thereafter. (b) A second alternative would be to select 20 per cent of the new routes at random during each of the next five years, after which the entire nation-wide sampling would be on a statistically acceptable basis of randomization.

6) After the nation-wide sampling has been randomized, it may be necessary to select a few new routes each year to replace those routes on which the census technique cannot be applied. Suburban development, new main highways, airfields, and growth of population centers will make annual replacement of a few routes desirable.

SUMMARY

This paper compares results from call-count censuses of 141 original management routes to be censused nationally should be seven Southeastern States. Within the limitations of the call-count technique, the random routes were chosen after stratification into state strata. Both sets of routes were censused during the regular dove censusing period in 1957 by experienced cooperators who have censused the original management routes since 1951. Results indicate that the original management route sampling is positively biased, with higher than average dove population areas being sampled. Although differences between the mean numbers of doves heard calling on original management and randomly selected routes are small, the method of selection of routes to be censused nationally should be revised so that call-count data will have application for both time and area comparisons. Results indicated that stratification by ecological zones is a more efficient sampling designed than either stratification by state strata or completely random sampling. Suggestions are made for revision of the nation-wide call-count sampling.

LITERATURE CITED

COCHRAN, WILLIAM C. 1953. Sampling techniques. New York: John Wiley and Sons, Inc. 330pp.

DAVEY, STUART P. 1953. A study of the mourning dove in southern Michigan. M.S. thesis, Univ. of Mich. 40pp.

DUVALL, ALLEN J. AND CHANDLER S. ROBBINS. 1952. Investigations of methods of determining abundance of breeding mourning doves in certain eastern states. U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept., Wildl. No. 17:15–34.

FOOTE, LEONARD E. 1953. Suggestions for a mourning dove management program. Paper presented at Southeastern Assoc. Game and Fish Comm. meeting, Chattanooga, Tenn., Oct. 11pp.

———. 1957. Suggestions for a mourning dove management program. 14pp. (privately printed, Marietta, Ga.)

——— AND HAROLD S. PETERS. 1952. Introduction, *in* Investigations of methods of appraising the abundance of mourning doves. U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept., Wildl. No. 17:1–4.

KERLEY, CLAYTON. 1952. The call-road count as an index to breeding populations of the mourning dove in east Tennessee. U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept., Wildl. No. 17: 8–14.

MCGOWAN, TERRY A. 1952. An intensive study of the call count as a census method for mourning doves on the Georgia Piedmont. U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept., Wildl. No. 17:4–7.

———. 1953. The call count as a census method for breeding mourning doves in Georgia. J. Wildl. Mgmt., 17(4):437–445.

PETERS, HAROLD S. 1952. A summary of mourning dove call count investigations in Ohio. U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept., Wildl. No. 17:35–46.

SNEDECOR, GEORGE W. 1956. Statistical methods. (5th edition.) Ames: Iowa State College Press. 534pp.

SOUTHEASTERN ASSOCIATION OF GAME AND FISH COMMISSIONERS. 1957. Mourning dove investigations, 1948–1956. Southeastern Assoc. Game and Fish Commissioners (Columbia, S.C.), Tech. Bull. No. 1. 166pp.

WAGNER, FRED H. 1952. Preliminary investigations on mourning dove index and survey methods in Wisconsin. U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept., Wildl. No. 17: 47–53.

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REPRODUCTION AND AGE DISTRIBUTION OF BLACK-TAILED JACK RABBITS IN KANSAS[1]

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The black-tailed jack rabbit (*Lepus californicus*) is an important mammal in the agricultural economy of western Kansas because of its crop depredations. During years when these hares are abundant, they are heavily hunted both for sport and in an attempt to reduce the population. During a 5-year drought (1952–56), these jack rabbits were more numerous in Kansas than at any time since the drought of the mid-1930's (Bronson, 1957). Because of this increase to pest proportions and a lack of information about jack rabbit ecology in the Central Plains States, a comprehensive study of this animal was initiated in the summer of 1956. Data are presented here on its reproduction and age distribution from July 1956 through November 1957. The results are compared with similar studies of this species (Vorhies and Taylor, 1933; Lechleitner, 1956) and examined to determine their usefulness in understanding the population fluctuations of this species in Kansas.

Materials and Methods

The 17-months' collections totaled 904 specimens. Over 75 per cent of these animals were killed in the Arkansas River valley and in a sand-hill region in eastern Kearny County, Kansas. Jack rabbits were taken between the hours of 3 P.M. and 3 A.M. by means of a .22-caliber rifle or occasionally a 12-gauge shotgun. A 6-volt spotlight was used to aid in collecting after sunset. Weights and measurements were taken, the left humeri removed, and the testes and female reproductive tracts removed and fixed in 10 per cent buffered Formalin. Notes were taken on the condition of the nipples, the relative amounts of mammary tissue, and the size and condition of the internal and external genitalia. Age was determined by comparing the size and condition of the genitalia and by the epiphyseal-closure method. The time between death and examination ranged from a few minutes to 14 hours, with a median time of about 4 hours.

In the laboratory, the epididymides were removed from preserved testes, and each pair of testes was then weighed on a "Gramatic" balance. The numbers of sperm were estimated by using a 0, 1, 2, 3, or 4 scale of increasing relative abundance. Ovaries were sectioned with a razor blade and examined macroscopically to determine the diameter of the larger peripheral follicles and the numbers of rupture sites and corpora lutea. Crown-rump and zygomatic-breadth measurements were taken on all embryos where possible, and the larger embryos were sexed. Evidence of resorption was recorded. A mean ovary-size index (length × width) was obtained for each female, but little information was gained from analyses of the resulting data. Analyses of data taken from placental-scar counts, numbers of peripheral follicles and corpora albicantia proved of no value in this study. According to Hall (1955), these specimens are referable to the subspecies *L. c. melanotis*.

Results

Sex ratios.—Sex ratios of adults, juveniles, and fetuses were not significantly different from a 100:100 ratio when analyzed separately, aggregated, or when collections of adults were analyzed according to reproductive versus nonreproductive season (Table 1).

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TABLE 1.—ADULT, JUVENILE, AND FETAL SEX RATIOS AND 95 PER CENT CONFIDENCE LIMITS

	Number Collected	Males/100 Females	Per Cent Males	95 Per Cent Limits of Error (% males)
Juveniles	473	107	52	± 4.5
Adults				
Feb.–August	285	100	50	± 5.8
Sept.–January	146	111	52	± 8.1
Subtotal	431	103	51	± 4.7
Total	904	105	51	± 3.3
Fetuses	81	132	57	±10.8

Breeding season.—A definite annual breeding cycle was exhibited by these hares in southwestern Kansas. This cycle was demonstrated in males by an increase and then a decrease in average paired-testes weights and in monthly comparisons of sperm counts (Table 2). Cessation of testicular activity occurred by September in both 1956 and 1957. However, the onset of sperm production differed considerably for the two periods studied. In 1956, sperm production had begun in some individuals by December, and no animals showed any evidence of testicular activity during the period from September through November. In 1957, sperm production ceased only during September. Average testes weights were also much higher in October and November of 1957. Paired-testes weights of males considered capable of breeding ranged from 3.9 to 21.3 grams. Sperm production was generally confined to those males with paired-testes weights of five grams or over.

Pregnant females were collected from the last week of January 1957 until August 1957 (Table 3). The breeding season indicated was approximately 220 days. The low percentage (6 per cent) of females pregnant in February 1957 was probably the result of sampling error, because five of the six non-pregnant specimens taken in March had been bred in February.

Fetal counts.—The data presented to estimate the litter size at the time of birth and the average annual production refer only to the 1957 breeding season because data

TABLE 2.—MEAN TESTES WEIGHTS OF ADULT MALES, PERCENTAGE WITH SPERM IN TESTICULAR SMEARS AND PERCENTAGE WITH COMPARATIVE SPERM COUNTS OF THREE OR FOUR IN EPIDIDYMAL SMEARS

Date Collected	Number Collected	Mean Testes Weight (Grams)	Epididymal Smears	Testicular Smears
1956				
July	23	13.3	100	100
August	12	5.5	54	31
September	10	2.3	10	0
October	7	1.8	0	0
November	12	2.4	0	0
December	8	4.0	15	15
1957				
January	26	8.7	100	100
February	26	10.4	100	100
March	21	12.7	100	100
April	28	14.5	100	100
May	16	14.9	100	100
June	11	15.1	100	100
July	1	13.1	100	100
August	4	13.2	100	75
September	3	2.0	0	0
October	7	4.1	14	29
November	4	8.8	50	75

TABLE 3.—NUMBERS OF ADULT FEMALES COLLECTED, NUMBERS PREGNANT, AND PERCENTAGE PREGNANT

Date Collected	Number Collected	Number Pregnant	Percentage Pregnant
1956			
July	14	11	79
August	13	5	38
September	13	0	0
October	6	0	0
November	11	0	0
December	12	0	0
1957			
January	16	1	6
February	16	1	6
March	17	11	65
April	38	34	90
May	20	15	75
June	13	8	62
July	5	2	40
August	7	6	86
September	3	0	0
October	4	0	0
November	3	0	0

were not obtained for the entire 1956 season. The average number of fetuses per pregnant female was calculated only from litters that were half term or older. A crown–rump measurement of 40 millimeters was assumed to be half term (Lechleitner, *op. cit.*). Thirty-two pregnancies consisted of 83 fetuses for an average of 2.6 (± 0.19 S.E.) per litter. Number of fetuses per pregnant female ranged from one to five, with 55 per cent of the litters older than half term containing either two or three embryos. Fetal counts were smaller during the first part of the breeding season (average for February was 1.0; April, 2.1; and June, 3.3).

Average annual production.—The average number of young per year produced by a female may be calculated by using the percentage of females not pregnant during the breeding season as an indication of the average time between pregnancies in the population. During the 220-day breeding season, 66 per cent of the adult females were pregnant. By multiplying the 34 per cent not pregnant by the 43-day mean gestation period (Haskell and Reynolds, 1947), an average period of 58 (43 + 15) days was required to produce one litter. Dividing the 220-day breeding season by the 58-day period results in an estimated 3.8 litters produced per female per year. The average annual production would be $3.8 \times 2.6 = 9.9$ (± 0.74 S.E.) young per female per year. This estimate, however, does not take into consideration that a certain proportion of the pregnancies examined would not have reached full term due to resorption of the litter in its entirety. The prenatal loss of members of a litter was believed to have been effectively taken into consideration when the mean number of fetuses was calculated only from healthy pregnancies older than half term. Lechleitner (*op. cit.*) presented a method to correct for resorption of entire litters in calculating the average number of litters produced. All requirements for utilizing his method could not be satisfied in this study (i.e., significant results were not obtained when comparing the losses of entire litters before and after midterm). The true average number of young born to a female in the population studied would probably be slightly below the calculated 9.9 average obtained above.

Prenatal mortality.—As reported for other lagomorphs, prenatal mortality was found to be heavy. The pregnant females examined had, by corpora lutea and rupture-site counts, ovulated 259 ova and produced 218 healthy embryos. This apparent 16 per cent loss is a minimum estimate because, as stated by Brambell (1944), the difference between the number of ova shed and the number of embryos gives an inaccurate estimate of total loss unless allowance is made for the stage of pregnancy when the loss occurred. Actual observed resorption of any or all members of a litter was found in 15 per cent of the litters and included 8 per cent of the total number of embryos. During the study period, 8 per cent of the litters examined were undergoing resorption of all embryos. None of the resorbing litters that could be aged with reasonable accuracy were older than half term. Lechleitner (*op. cit.*) found the greatest loss of entire litters during the initial half term of pregnancy. A comparison of the frequency of occurrence of pregnancies older than half term with those less than half term

TABLE 4.—MONTHLY AGE DISTRIBUTION OF 904 SPECIMENS

	1956						1957										
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Number collected	72	90	76	71	61	50	53	52	38	66	38	29	27	42	39	49	51
Number adults	37	25	23	13	23	20	42	42	38	66	36	24	6	11	7	11	7
Number juveniles	35	65	53	58	38	30	11	10	0	0	2	5	21	31	32	38	44
Per cent juveniles	49	72	70	82	62	60	21	19	0	0	5	21	78	74	82	78	86

gave nonsignificant results in this study. There were 46 litters in the early stages of pregnancy and 32 litters older than half term ($X^2 = 2.50$, 1 *D.F.*, $P = 12$ per cent).

Evidence of an abnormally high incidence of resorption was found in March of 1957. Seventeen adult females were collected 2 days after the end of a 3-day blizzard of exceptional intensity. Four of these females were in the process of resorbing their entire litters, and two others had recently resorbed or aborted. This would indicate that periods of stress, in this instance a 3-day blizzard, may cause the loss of many entire litters.

Young-of-the-year breeding.—Only one male aged as a young of the year showed evidence of testicular activity during or immediately after the same breeding season in which it was born. On the basis of this one individual, taken in September 1956, it would seem that a minimum age of 6 or 7 months is required before young males begin to produce sperm. Only one female young of the year, collected in September of 1957, showed any evidence of having been bred. This female had one receding corpus luteum and was in the process of resorbing an early-stage embryo.

Aging and age distribution.—In general, jack rabbits collected in Kansas could be aged by the epiphyseal-closure method through November. Closure of the proximal epiphysis with the diaphysis had not occurred in any of the 38 young of the year collected in October of 1957. Closure had occurred in 10 (23 per cent) of the 44 young of the year taken in November of 1957, but there remained a discernible narrow white line on each humerus of these 10 individuals. Since the first litters were born in March, it is apparent that epiphyseal closure occurs in this lagomorph at approximately 8 months of age. From December until breeding commenced, young-of-the-year females could be classified as such by the small size and condition of their reproductive tracts. All males taken during December and January were classified as adults. Table 4 summarizes the age distribution data. The fall age index, which consisted of the average age ratio for September, October, and November, was 71 per cent young of the year in 1956 and 82 per cent in 1957 ($X^2 = 4.8$, 1 *D.F.*, $P = 3.5$ per cent).

Abnormalities and miscellaneous.—No case of superfetation or of pseudopregnancy was found. One case of either polyovulation or transmigration of an ovum was found. A significant difference (5 per cent level) was noted in the number of embryos in the left and right horns of the uterus. The left:right ratio of embryos collected during the study period was 137:103 ($X^2 = 4.8$, 1 *D.F.*, $P = 3.5$ per cent).

DISCUSSION

The reproductive biology of the black-tailed jack rabbit in Kansas as reported here was different in many respects from that found in similar studies in Arizona and California. Vorhies and Taylor (*op. cit.*) found jack rabbits breeding in all but 2 months of the year in Arizona and estimated seasonal production at eight young per female. Lechleitner (*op. cit.*) found pregnant females in all months and calculated a seasonal production of 9.8 young in California. In both of these studies, 100 per cent of the females were pregnant during certain periods of the year. The reason for the annual reproduction of this species being restricted to 7 months of the year in Kansas rather than as found in California and Arizona was undetermined. The more

severe winter climate of the Central States and/or a photoperiod difference may be causes for this decided difference in the length of the breeding season. Another factor causing fewer litters to be produced in Kansas than in the other states was the lack of consistent postpartum breeding. Never were 100 per cent of the females pregnant in Kansas. However, the larger average number of fetuses per pregnant female calculated in this study (2.6 ± 0.19 S.E. as compared to 2.2 in Arizona and 2.3 in California) compensated for the smaller number of litters. Because of this compensating factor, the total annual production figures estimated by the three studies were not greatly different.

This jack rabbit is apparently not cyclic in Kansas. The information available (Wooster, 1935) indicates that drought periods are accompanied by marked increases in the jack rabbit population. The annual precipitation for the region where specimens were collected and where population work was conducted in conjunction with this reproduction study averaged 11.2 inches per year during the 5-year drought of 1952–56, compared to a normal of 16.8 for the region. The precipitation totaled 7.5 inches in 1956 and 21.9 inches in the first 11 months of 1957, the year in which the drought ended and the population was thought to have begun to decline. Wooster (*ibid.*), when reporting the population increase of these animals in Kansas during the drought of the 1930's, theorized that an increase in the survival of the young during dry years was responsible for population increases. The fall age indices, which were 71 per cent young of the year in 1956 and 82 per cent in 1957, are significantly different ($X^2 = 4.8$, 1 *D.F.*, $P = 3.5$ per cent). The higher index was found after the drought was broken and in a year when the total precipitation was three times as much as in the preceding year. This would indicate that (a) there were fewer young born in the dry year than in the wet year, or (b) there was better survival of young in the wet year. Since the jack rabbit population in Kansas is known to increase during droughts, it may be that such increases are, at least in part, the result of better survival of the members of the population during the dry years. Further work is needed to clarify this point.

SUMMARY

Data are presented on the reproduction and age distribution of the black-tailed jack rabbit in Kansas based on 17 monthly collections totaling 904 animals. This species exhibits a definite annual breeding cycle in Kansas. In 1957 this breeding season was roughly 220 days and during that period an estimated average of 3.8 litters was produced per female. The mean number of fetuses per pregnant female was 2.6, resulting in an estimated average seasonal production of slightly below 9.9 young per female. Breeding by young of the year was negligible. Eight per cent of the embryos examined were undergoing resorption. The fall age ratio was 71 per cent young of the year in 1956 and 82 per cent in 1957. The usefulness of the data in understanding jack rabbit population fluctuations in Kansas was discussed.

The reproductive biology of this animal in Kansas differed in the following aspects from the results of similar studies in Arizona and California: (a) breeding was restricted to a 7-months' period in Kansas; (b) consistent postpartum breeding was not found; and (c) a larger average fetal count was found in Kansas, which compensated for the limiting effects of the first two factors on comparative annual production.

LITERATURE CITED

BRAMBELL, F. A. ROGERS. 1944. The reproduction of the wild rabbit *Oryctolagus cuniculus* (L.). Proc. Zool. Soc., 114:1–45.

BRONSON, F. H. 1957. The ecology of the black-tailed jackrabbit in southwestern Kansas. Unpub. Master's thesis. Kansas State College of Agriculture and Applied Science. 84pp.

HALL, E. RAYMOND. 1955. Handbook of mammals of Kansas. Univ. Kans. Mus. Nat. Hist., Misc. Publ. No. 7. 303pp.

HASKELL, H. S. AND H. G. REYNOLDS. 1947. Growth, developmental food requirements and breeding activity of the California jackrabbit. J. Mammal., 28:129–136.

LECHLEITNER, R. R. 1956. The black-tailed jackrabbit on the Gray Lodge Waterfowl Area, California. Unpub. Ph.D. thesis. Univ. California, Berkeley. 161pp.

VORHIES, C. T. AND W. P. TAYLOR. 1933. The life histories and ecology of jackrabbits, *Lepus alleni* and *Lepus californicus* in relation to grazing in Arizona. Univ. Arizona, College Agric. & Exp. Sta., Tech. Bull. No. 49. 117pp.

WOOSTER, L. D. 1935. Notes on the effects of drought on animal populations in western Kansas. Trans. Kans. Acad. Sci., 38:361–362.

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ANNUAL MORTALITY IN A BANDED BOBWHITE POPULATION[1]

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The primary purpose of this paper is to test the hypothesis that the annual mortality rate of an unhunted population of bobwhite (*Colinus virginianus*) does not differ from that of a hunted population. The most reliable information on annual mortality of the bobwhite has come from analyses of age ratios, derived either from hunted samples (Leopold, 1945; Bennitt, 1951) or from trapped samples (Buss, Mattison, and Kozlik, 1947). In general, these age-ratio studies have included data from limited seasons, such as midwinter or an autumnal hunting season. The present study includes data gathered in all months. Age- and sex-ratio analyses were based on 1,156 banded bobwhites trapped from January 1950 through March 1957 (Table 1).

The study area was located in Boone County, central Missouri, and included the Ashland Wildlife Research Area and its immediate environs. The Ashland area is a refuge comprising 2,240 acres of submarginal land, with farms to the north and west and woods to the south and east. Most of the trapping and banding operations were conducted on the refuge itself, and the population had been shown to be largely self-contained (Murphy and Baskett, 1952). Thus, although there was light hunting on land surrounding the refuge, all of the trapped birds in this paper are considered to be part of a refuge population. Essentially a stable habitat, the entire study area has undergone no major land-use changes during the course of the banding program. The study area is not high-quality quail

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TABLE 1.—DISTRIBUTION OF ORIGINAL BANDING RECORDS OF 1,156 BOBWHITES, 1950–57

Year	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Totals
1950	54	28	44	14	12	15	3	2	21	21	15	19	248
1951	47	28	37	12	23	44	41	20	37	12	19	12	332
1952	—	—	—	8	20	24	12	10	—	—	—	—	74
1953	25	27	5	—	—	—	—	—	43	50	7	17	174
1954	—	—	—	42	23	10	20	25	16	—	—	—	136
1955	—	—	—	—	12	18	—	6	13	4	2	—	55
1956	11	24	10	—	7	2	1	—	30	16	—	—	101
1957	—	—	—	20	10	6	—	—	—	—	—	—	36
Totals	137	107	96	96	107	119	77	63	160	103	43	48	1,156

range; cover seems adequate, but food may be limiting in winter.

METHODS

Although several workers gathered the data that were used in this study, field techniques were uniform throughout the various phases of the trapping and banding program. These field methods are described briefly below. Murphy and Baskett (*ibid.*) provided a more detailed description.

In summer a modified version of the "cock-and-hen" trap described by Stoddard (1931:446) was employed. A concentration of whistling males was located, and a trap baited with a decoy female was set nearby. Whistling by the decoy and the investigator usually resulted in a catch of one or more males. Wild hens were caught infrequently during the summer.

In winter the "cock-and-hen" traps baited with mixed grains proved to be the most successful. A covey was located, its general range determined, and several traps were set.

All trapped bobwhites were banded. Adults were distinguished from juveniles and yearlings by the characteristic differences in the upper primary coverts (Leopold, 1939).

AGE RATIOS

Age-ratio analyses were based on 1,546 captures, and recaptures were totaled by months for all years. Following its initial capture, a bird was included in the totals for all the succeeding months in which it was recaptured, but only once in any given month. The age-ratio data for all months consist of adults, and young from the previous summer's hatch. Data secured from the middle of April to the first of August were almost exclusively from male birds, because of the use of decoy females in summer trapping. August and September data were omitted from the totals to avoid molting birds and the confusing overlap between age groups. All birds of unknown sex were omitted.

To determine whether trapping was selective with respect to age, we made an analysis of repeat records, an approach suggested by Borror's (1948) paper on the white-throated sparrow (*Zonotrichia albicollis*). In the present analysis a bird was considered to repeat if it was recaptured within the banding year (October through July). The hypothesis that the young and adults belonged to a single population, equally subject to recapture, was tested by means of chi-square, using the recapture data in Table 2. There was no significant difference between the two groups (chi-square = 3.41 with 3 *d.f.*). Thus, we can assume that the trapping was not selective with respect to age.

TABLE 2.—REPEATS IN YOUNG AND ADULT BOBWHITES

Number of Repeats	Young		Adults	
	Number	Per Cent	Number	Per Cent
0	621	63	133	69
1	181	19	32	17
2	79	8	11	6
3 or more	102	10	15	8
Totals	983	100	191	100

A stable population is a prerequisite for the use of age ratios as an index to annual mortality. The Ashland population was fluctuating rather than stable. However, there was no consistent trend, and 7 years of fluctuation are herein considered to be equivalent to stability.

The percentage of young birds found during each banding year is shown in Fig. 1. Differences in these annual ratios were significant (homogeneity chi-square = 26.025 with 7 *d.f.*). The fluctuations in the annual age ratios indicate corresponding changes in annual productivity and mortality rates. However, these changes show no consistent upward or downward trend, and pooling data from all years compensates for annual fluctuations in productivity and mortality rates. The resulting theoretical population has characteristics identical with none of the individual years concerned. However, statistics derived from this population can be most useful in providing a working knowledge of the dynamics of the species.

Age-ratio data were grouped in bimonthly periods (Table 3). There was no significant

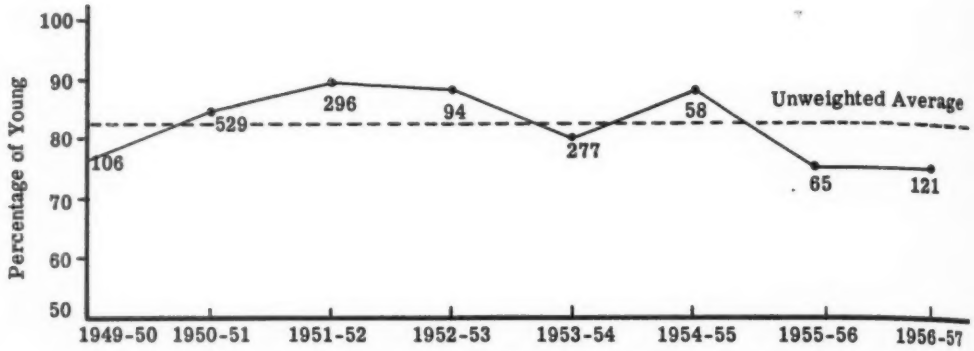

FIG. 1. Bobwhite age ratios, 1950–57 (numbers on graph show sample size).

difference in the percentage of young throughout the banding year (homogeneity chi-square = 5.251 with 4 *d.f.*).

Since there was no significant change in the young–adult ratio after October 1, it appears that survival rates for young and adult bobwhites were the same after this date. Thus, pooling the data from all months is justified.

In pooling the age-ratio data, an unweighted average of years was used, for, despite variations in sample size, data from each banding year represent the best estimate of that particular year class. The unweighted average percentage of young in the theoretical population is 82 per cent, which implies an annual adult mortality rate of 82 per cent.

Bennitt (*op. cit.*) found a drop in the percentage of young amounting to 0.6 per cent per week over the 8-week hunting season in Missouri (November–December). He concluded that "[the change] is enough to show that young birds, even if fully grown, are slightly more vulnerable to shooting than old birds." Rosene (1957) found a drop in the percentage of young in a shot sample of South Carolina bobwhites as the season progressed (from an average of approximately 80 per cent in December and January to 74.7 per cent in February). In a preliminary report, Reeves (1951) found just the opposite in a trapped sample of Indiana bobwhites—a drop in the percentage of adults from a high of 18 per cent in the fall to 15 per cent by midwinter to 8 per cent by early summer.

Thus, perhaps the most important point for consideration resulting from the age-ratio analysis of the Ashland population is that once a bird reached its first October (2–4 months of age), its chances of survival apparently did not change, and young in their first winter were dying at the same rate as the adults (82 per cent per year). This is in direct contrast to Emlen's (1940) study of the California quail (*Lophortyx californica*), where a progressive change was found in the age ratios throughout the year.

Selected age ratios of bobwhites (i.e., those based on studies that have large samples taken over a number of years) are shown in Table 4. Data presented in this table make it apparent that annual mortality rates are as high in refuge populations as they are in hunted populations. This suggests that hunting is functioning only

TABLE 3.—BIMONTHLY VARIATIONS IN PERCENTAGES OF YOUNG IN A BANDED BOBWHITE POPULATION, 1950–57

	Oct.–Nov.	Dec.–Jan.	Feb.–Mar.	Apr.–May	June–July
Adults	43	65	47	39	62
Young	268	274	264	215	269
Totals	311	339	311	254	331
Per cent young	86	81	85	85	81

TABLE 4.—SELECTED AGE RATIOS IN BOBWHITES

Place	Source of Data	Sample Size	Per Cent Young	Reference
Missouri	Hunters	1,633	77	A. S. Leopold, 1945
Missouri	Hunters	51,178	82	Bennitt, 1951
Missouri	Traps–refuge	1,546	82	This study
Wisconsin	Traps–refuge[1]	593	83	Buss, *et al.*, 1947

[1] Study area located at the northern periphery of the species' range and in a county entirely closed to hunting throughout the period of observation.

as an alternate cause of the high annual mortality in the bobwhite. Closed seasons, therefore, would seem to have little value as a method for increasing bobwhite populations.

Average longevity, or the average expectation of further life, was calculated by Lack's (1954) formula of $\frac{2-m}{2m}$ where m equals the percentage of annual mortality. With an annual mortality rate of 82 per cent, average life expectancy after the first October of life would be about 8½ months. An annual mortality rate of 82 per cent also implies that about one bobwhite in 1,000 would survive to its fifth year. In this study, one of the 1,156 banded bobwhites was shot in its fifth year. This is the greatest longevity recorded in the study.

SEX RATIOS

The sex-ratio analyses were based on the same captures and recaptures used for the age ratios, but because of the obvious bias of summer "cock-and-hen" trapping in favor of males, sex-ratio data were drawn only from the 961 captures and recaptures made from October through March.

An analysis of repeats in the sexes was also made. However, to guard against the presence of a differential sex mortality, a bird was called a repeat only if it was recaptured within a month of initial capture. Data are from birds captured from October through February (Table 5). A comparison of the relative frequency of repeats between males and females revealed no significant difference between the observed and expected (chi-square = 0.026 with 1 *d.f.*). This strongly suggests that the sexes were equally responsive to the traps.

TABLE 5. REPEATS IN MALE AND FEMALE BOBWHITES

	Number	Repeats	Per Cent Repeats
Males	283	63	19
Females	232	53	18

Sex ratios were remarkably constant from year to year; there was no significant difference among years (homogeneity chi-square = 9.022 with 5 *d.f.*). As with the age ratios, the sex ratios under consideration are from a theoretical population (data pooled from all years).

Sex ratios showed no significant difference between months (homogeneity chi-square = 5.488 with 5 *d.f.*). The sex ratio (data from all months and years) in 155 adults was 167 males per 100 females [= 63 per cent males]; in 806 young it was 121 males per 100 females [= 55 per cent males]. In both age groups the deviation from a 50:50 ratio was significant (chi-square = 9.812 and 7.540 respectively, with 1 *d.f.*). The difference in the sex ratio between young and adults was significant only at the 92 per cent level (chi-square = 3.19 with 1 *d.f.*).

Distortion of the sex ratio in bobwhite, indicating better survival of males, is widely reported in the literature. There have been two principal theories as to when the discrepancy in the sex ratio arises. Stoddard (*op. cit.*:94) thought that there was a higher mortality among hens during autumn and winter. Three studies that show the discrepancy in the sex ratio to be largely confined to the adult segment of the population are listed in Table 6. All these authors concluded that distortion of the sex ratio was probably due to greater hen mortality during the nesting season (spring and summer).

TABLE 6.—PERCENTAGES OF MALES AMONG YOUNG AND ADULT BOBWHITES

Reference	Percentage of Males among Young	Percentage of Males among Adults
A. S. Leopold (1945)	50.5	62
Bennitt (1951)	50.5	59
Buss, *et al.* (1947)	54	63

In the Ashland population the young showed a significant deviation from a 50:50 ratio. If we assume a 50:50 sex ratio at hatching, it would seem that some distortion was arising before the first breeding season. Precisely when or how is impossible to say from the data at hand. The difference in the sex ratio between young and adult segments of the population suggests further distortion between the end of one trapping period (March) and the beginning of the next (October); the nesting season with its greater hazards for the hen could be the explanation.

EMIGRATION RATE

The rate of disappearance of an animal population is determined not only by mortality but also by the rate of egress from the area under study. At no time during the Ashland banding program was there an adequate, direct measure of egress (Murphy and Baskett, *op. cit.*; Lewis, 1954). The work of Jackson (1948) on the tsetse fly (*Glossina morsitans*) suggested a possible approach to an indirect determination of egress.

The primary data for the analysis consisted entirely of recaptured, banded bobwhites. If there was a uniform probability of recapture among all members of the population, then the percentage of banded birds recaptured after t units of time, compared to the percentage recaptured at t-1 units, gives a measure of mortality plus emigration in one interval. These mortality-plus-emigration rates should be constant and recaptures should decrease logarithmically with time.

That the traps were nonselective with respect to all portions of the population cannot be shown with certainty. However, the sexes and the age groups were sampled in a nearly random manner. Other possible sources of bias would include trap-shy and trap-prone birds, and birds on the edge of the area of trapping influence. These and other potential sources of nonrandomness limit the precise calculation of emigration rate by this method, but a preliminary calculation seems to be desirable.

A total of 1,124 recaptures were made on the 1,156 banded bobwhites. By grouping the recaptures in monthly intervals (recaptured within a month, 1–2 months, etc., up to 18 months), the following "extinction" series is obtained: 424–189–149–92–72–52–44–34–18–11–13–15–5–3–2–0–0–1.

The equation for the regression is given by $y = a + bt$ where:

$y = log_{10}$ of recaptures (R) at time t,
t = time in monthly intervals (0.5, 1.5, etc.),
a = a constant (y intercept),
b = slope of regression (–0.15345).

The regression coefficient was highly significant ($s_{y.x} = 0.403$). The disappearance rate and the number of birds theoretically available for recapture at time t is given by

$y = 2.59511 - 0.15345t$ or
$R = 393.6 \times 10^{-0.15345t}$.

To calculate the disappearance rate for one year, $t = 12$ (months) was substituted in the above equation as follows:

$$12 \times -0.15345 = 10^{-1.8414}$$
$$= 0.01441 \text{ (probability of recapture after one year).}$$

Thus, the disappearance rate is 1–0.1441, or 98.56 per cent per year, and the number of birds theoretically available for recapture under average trapping intensity at time 0 is the antilog of a, or 394. The curve plotted from these data is presented in Fig. 2.

The average annual mortality (82 per cent) and the over-all annual disappearance rate due to mortality plus egress (98.6 per cent) have been calculated by two independent methods. If the assumptions of these two methods are accepted, then the annual rate of egress must be 98.6–82 or 16.6 per cent.

The advantage of dealing with recaptures only is that variations in the probability

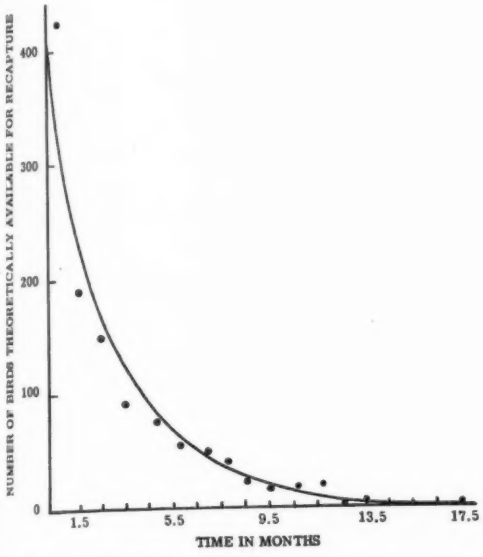

FIG. 2. Extinction curve for the banded population.

of recapturing a bird because of changes in trapping intensity and effectiveness average out in time. Thus, the method presented above, although particularly well suited to the Ashland data, could conceivably be used in other studies where a long, somewhat intermittent trapping program is carried out on a resident population.

SUMMARY

A trapping and banding program was maintained for 7 years in a bobwhite population on a central Missouri refuge. The population was fluctuating, but the cumulative data approached theoretical stability. Analysis of repeat records revealed no bias of trapping methods with respect to age and sex. Age-ratio data from 1,546 captures and recaptures pooled for all years indicated an average annual mortality of 82 per cent. There was no significant change in the age ratios from October through July, indicating that young in their first winter were dying at the same rate as were adults. Calculated life expectancy after the first October of life averaged 8½ months. The greatest longevity recorded in this study was for a banded bobwhite shot in its fifth year. A regression analysis of 1,124 recaptured bobwhites grouped by monthly intervals gave an annual disappearance rate of 98.6 per cent, of which 82 per cent was attributed to mortality and 16.6 per cent to egress from the area of trapping activity. This study provides another source of evidence that in the bobwhite, with its high annual mortality rate, hunting is merely a substitute for other forms of natural mortality.

REFERENCES CITED

BENNITT, R. 1951. Some aspects of Missouri quail and quail hunting 1938–1948. Mo. Conservation Comm., Tech. Bull. No. 2. 51pp.

BORROR, D. J. 1948. Analysis of repeat records of banded white-throated sparrows. Ecol. Monog., 18:411–430.

BUSS, I. O., H. MATTISON, AND F. M. KOZLIK. 1947. The bobwhite quail in Dunn County, Wisconsin. Wis. Conservation Bull., 12(7):6–13.

EMLEN, J. T., JR. 1940. Sex and age ratios in survival of the California quail. J. Wildl. Mgmt., 4:92–99.

JACKSON, C. H. N. 1948. The analysis of a tsetse-fly population. III. Ann. Eugenics, 14:91–108.

LACK, D. 1954. The natural regulation of animal numbers. Oxford:Oxford Univ. Press. 343pp.

LEOPOLD, A. S. 1939. Age determination in quail. J. Wildl. Mgmt., 3:261–265.

———. 1945. Sex and age ratios among bobwhite quail in southern Missouri. J. Wildl. Mgmt., 9:30–34.

LEWIS, J. B. 1954. Further studies of bob-white mobility in central Missouri. J. Wildl. Mgmt., 18:414–416.

MURPHY, D. A. AND T. S. BASKETT. 1952. Bobwhite mobility in central Missouri. J. Wildl. Mgmt., 16:498–510.

REEVES, M. C. 1951. Sex, age, and weight studies of Indiana bobwhite quail. Outdoor Indiana, 18(8):10–11.

ROSENE, W., JR. 1957. Analysis of age, sex ratios and molt progress in a bobwhite population. Typewritten ms. filed in U.S. Fish and Wildlife Service, Gadsden, Ala. 22pp.

STODDARD, H. L. 1931. The bobwhite quail; its habits, preservation and increase. N.Y.:Charles Scribner's Sons. 559pp.

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AUTUMN THOUGHTS OF A HUNTER

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Hunting and fishing are sports that participants are inclined to take for granted. We are now beginning to realize that game and fish, and access to them, are not things that we can afford to leave to chance. How many have also stopped to think that hunting and fishing usually culminate in the death of some animal, that at the very least an attempt is made to molest or injure, and that there are many people who disapprove of all such things?

A recent survey in the United States (U.S. Fish and Wildlife Service, 1956) showed that in 1955 somebody in one of every three households hunted or fished. There were some twelve million hunters and twenty-one million fishermen. Included in both totals were eight million people who did both, for a grand total of twenty-five million people whose recreation was found in killing things. Most United States statistics apply to Canada, with due allowance for the fact that in the States there are ten times as many people. We are, therefore, on this continent, a large company, and we are not likely to be deprived of our sport in a hurry; but if one reasonable man speaks against us, we owe it to ourselves to seek the truth.

Down through the years the greatest writers of poetry and prose, the singers, dancers, painters, and sculptors, have found inspiration in field sports. The hunter, said the ancients, is not the one who will be found wanting in due reverence to the gods. The hours spent angling are not reckoned against a man's life span. "For," says Xenophon, "all men who have loved hunting have been good." The voices that have been raised against us have been charged with emotion, coming, not as they pretend, from philosophical heights, but from tight compartments, insulated from reality. For this reason, sportsmen have scorned them. On this continent there is no awakening of sympathetic responses from such dangerous passions as the class hatreds of Europe. From a distance it is easy to see the kinship of the perennial anti-blood sports bills in the British parliament to the Cromwellian ban on bear-baiting, which, as Macaulay said, the Puritans disliked not because it gave pain to the bear, but because it gave pleasure to the spectators. We do not provoke criticism on such grounds.

We are not, however, invulnerable, even to emotional propaganda. This was brought home to me as I watched a huddle of university professors on our Canadian television trying to argue propositions submitted to them by the viewing public. On this occasion the proposition was a statement by a former Toronto journalist, the late J. V. McAree, to the effect that anyone who could go out and kill innocent creatures for fun had something wrong with him, and in fact had not grown up. I was especially interested because I had just finished reading an opposite view (*in* Voss, *et al.*, 1955), expressed in similar terms, by Gunther Schwab, poet and writer of the old festival city of Salzburg, who said that the chase should be only for the mature, others not being equipped to appreciate it. The professors all promptly agreed with McAree, and, in far less time than it takes to write it, they were quoting each other, until the whole thing was going round in a nice tight little circle, like a stuck phonograph needle. It must be admitted that this happy state is by no means rare in such programs, and must be the bane of masters of ceremony, as it may simply signify that the debaters know little and care less about the subject debated. It is neither fair nor useful to expose their ignorance and then cry, in Izaak Walton's words, "I here disallow thee to be a competent judge." The interesting fact is that an emotional statement evoked agreement, to the point where nobody, in an obviously intelligent group, even for the

sake of the program, was able to give the needle a push, much less turn the record over. To what degree do intelligent nonhunters accept the emotional arguments against hunting?

McAree's principal pronouncement on sport (McAree, 1951) may be cited to illustrate the quality of attacks on "blood sports." One could list many more like it. This one is printed in a secondary-school text, a fact that at one time caused me some apprehension. Now I am convinced that the interest in hunting is established before adolescence, and the young minds coming from at least one in three households would be resilient on this subject, however plastic in other respects. I am more concerned over the attitude of the textbook editors who chose this particular polemic from many. McAree justifies killing all predators, and all animals in any sense dangerous to man, but no others, and is sure that there are "proper ways" of regulating populations without hunting.

We have nothing to gain from controversy at the emotional level. In seeking truth in an emotionally charged atmosphere, one must be very careful of terms, and be as explicit as possible. In respect to the animals, we are dealing with two things, separable, although related. One is death. The other is pain. So far as man is concerned, we are dealing with the question of whether it is right or good for anyone to inflict either on a wild animal.

It might be contended that "right" and "good" are illusions, although whoever starts calling the things of the mind unreal may expect to end up in his own trap. If we abolished them, it would not matter what we did to animals, or what other people did to us. Society then would cease to exist, yet we know that it is older than our species. It must be confusing to try to reason from the premise of their nonexistence because the concept of a datum of excellence and justice, against which all conduct may be set, is part of the body and structure of the language in which our thoughts must be framed. It is equally difficult to abolish guilt, as some would do, in words that proclaim its existence. Without going into the arguments on this question, it is enough to say that I accept here the reality of the datum, and of the guilt implied in falling short of it. Lewis (1952) has argued it at some length in a discourse that I found stimulating. He sums it up by saying that humans "have this curious idea that they ought to behave in a certain way, and cannot really get rid of it," even though they "do not in fact behave in that way." Questions as to the nature, origin, variability, and absoluteness of this principle do not affect us here.

Thus, we may continue to speak of "right" and "good." As Lewis is a religious writer, I had hoped to get a religious slant on the question of animal treatment from him, especially as he deals with it in an earlier work (1940). It may be, he says, "that wild animals have no selves and no sufferings," in which case it would not matter what one does to them, but he leaves the question open. Domestic beasts, he says, are in a higher state, because they have achieved the true natural state of a beast, which is to be subordinate to man. This sort of rationalization carried to its logical conclusion is that of the proverbial Spanish peasant, who justifies his ill-treatment of beasts by saying, "¿Porqúe? ¡No es Cristiano!" My ethic forbids me such convenient justification. As a biologist, I think that a wild turkey has at least as much ego as a tame one. I would agree, however, that there is a stage in natural development beyond which there can hardly be much question of suffering. Anglers are not seriously accused of cruelty. At the same time, the perverse boy who pulls the wings off flies may have the intent to inflict suffering, and thereby come under our moral ban, even though flies do not suffer.

The intent is important, as we shall see later. Also, we must remember that, although both we and animals are alive and sentient, our living is only part of the life of an organic whole. In our other-wordliness we have lost the feeling of man's oneness with the earth, which modern faiths do not deny, but which early chthonic faiths

saw most clearly, witness (Eliade, 1958) the original semantic unity of man (*homo*) and soil (*humus*), mother (*mater*), and matter (*materies*). Biologists, and most of all, wildlife biologists, know that any thought of man that he is apart from the rest of the living world is a perilous delusion. Here we face that part of our problem that concerns death. Death is a fundamental part of life.

The killing of an animal by another is harmful only if it is out of harmony with the functioning of the whole organic complex. Many other human activities are disruptive, and we can look at the face of earth and see that man has failed more often than not to achieve harmony with the land. This, surely, is the kind of savagery that we must outgrow, if we are to find any well-being. This figure of speech, incidentally, is from McAree (*op. cit.*), and was applied to hunting.

A phrase that nowadays is tossed glibly at the hunter by his more sophisticated critics is the guiding principle of the gentle healer of Africa, Albert Schweitzer—*Ehrfurcht for dem Leben.* Untranslatable, as are all really profound expressions, it means both Honour and Awe for Life—much more than Reverence, as it is usually rendered. Schweitzer goes far beyond any question of pain: "A man is really ethical only when he obeys the constraint laid on him to help all life which he is able to succour, and when he goes out of his way to avoid injuring anything living. He does not ask how far this or that life deserves sympathy as valuable in itself, nor how far it is capable of feeling. To him life as such is sacred. He shatters no ice crystal that sparkles in the sun, tears no leaf from its tree, breaks off no flower, and is careful not to crush any insect as he walks. If he works by lamplight on a summer evening, he prefers to keep the window shut and to breathe stifling air, rather than to see insect after insect fall on his table with singed and sinking wings" (Schweitzer, 1923b: 254 *et seq.*).

Schweitzer realizes the conflict of such a concept with the exigencies of human existence. He says, "The ethic of reverence for life recognizes no such thing as a relative ethic. . . . All destruction of and injury to life, from whatever circumstances they may result, are reckoned by it as evil. . . . The absolute ethic of reverence for life makes its own agreements with the individual from moment to moment . . . [and] forces him to decide for himself in each case how far he can remain ethical and how far he must submit himself to the necessity of destroying and harming life and thus become guilty."

What his own decision would be in a rather critical case, he lets us know. He recognizes the similarity of his creed to the ahimsa of India, carried so far by the Jains, but says that it would be better to give cattle whose utility has ended a violent death than to let them starve (Schweitzer, 1936). At Lambarene he kept a gun, so he tells us, but used it only to shoot snakes and predatory birds (Schweitzer, 1922). The modern hunter's ethic would have justified him in destroying these creatures only as they were dangerous individually.

To me it is a relief to find the good doctor admitting the breech of his own law. The ice crystal, after all, is inanimate, and it would be better to stop working at night than to have the moth's "will to live" (and to reproduce) frustrated by an artificial light! We are brought to the old dilemma of the Pharisees, who, uncertain of what they might or might not do on the Sabbath, did nothing. In the one case there was a basic misconception of the Sabbath; and in the other, of life. Any concept of life that does not comprehend the whole organic cycle is inadequate. The reluctance to accept death, evidently a predominant Schweitzer characteristic (Russell, 1941), reveals an unseeing devotion to the vital spark. It is death that makes it glow, measure for measure.

At the risk of weighing this essay down with Schweitzer, I have quoted at length and must argue at length because he is one of the greatest thinkers of our time. His ideas cannot be ignored, especially as he has challenged (Schweitzer 1923b) his

followers to action on the treatment of animals, and we are sure to hear from them as his shadow lengthens. *Ehrfurcht for dem Leben* is no Pharisaism. Schweitzer (1923a, 1923b) is right in affirming that the decay (*Verfall*) of civilization (*Kultur*) is caused by the lack of a proper relationship between man and other organic life, and its restoration (*Wiederaufbau*) can come only when such a relationship is established. I think that wildlife biologists would substitute "loss" for "lack," and "re-established" for "established." Man has lived, and in some places still lives, in harmony with nature, and the hunter and angler still cling to strong lines that connect us with the harmonious past. It is much more than not stepping on ants. One man, whether husbandman or forester, with a piece of land under his control, as mankind truly controls the whole earth, may go through life side-stepping ants and begging forgiveness of every blade of grass his mower touches; and in spite of his *Ehrfurcht,* because he has no feeling for the organic community, for the real life under his control, his land will have less and less life as the years pass, until, after generations of his kind, it may indeed die. Millenia of ahimsa have seen, and indeed contributed to, a man-made death for miles of land in India; and as the world of life shrinks in on the teeming mass of people, its individual elements cannot help growing more worthy of "reverence," until one day the remnant may be truly *furchtbar* (awe-inspiring). Another man, and he is very likely to be a hunter, will see to it that he leaves his land more truly alive and fruitful than he found it. Whose is the true reverence? Of course, one has no right to modify Schweitzer's concept in a direction so obviously rejected by him, but it seems to me that he was reaching out toward Leopold's "ecological conscience" (Leopold, 1947) and equally advanced conception of conservation ethics (Leopold, 1938), which are much closer to the heart of the problem of civilization.

As a biologist, then, I can accept *Ehrfurcht for dem Leben* only when life is interpreted as being the whole interwoven and interdependent association of plants, animals and soil, and the death that I inflict is right if harmony is maintained. The destruction of a whooping crane, for example, which would imperil the position of the species in the living community, or the violation of a game law, which, if nothing else, is a breech of trust with my fellow men, would be wrong.

With this clearly understood, I should be happy to see mankind guided by Schweitzer's maxim. Then the deliberate disintegrating of the beauty and productivity of our earth, so often hailed as "the conquest of Nature," will be abhorred. The true hunter, in the words of the old European hunter's pledge, "honours the Maker in His handiwork," but his honour, and awe, and reverence too, does not exclude delight, even in a doomed snowflake, a plucked daisy—or a wild goose headed for the platter.

In many areas of our own culture and in most primitive cultures, the chase is an integral part of a life where true harmony between man and nature exists. For example, the rural landscape of England, with its hedges and copses and beautifully managed fields, is, basically, a sporting landscape. Without fox hunting, the hedges would come down; without pheasant shooting, the copses would disappear. That is the civilized extreme. In the more primitive communities, where the power to destroy the landscape is less developed, the emotional, religious, and artistic life of the community is based to a remarkable degree on wildlife, and the chase is esteemed whether or not it is necessary for sustenance.

There is nothing remarkable about this. Man evolved as a hunter (Heberer, 1951). Forerunners of man are rather well known now. In South Africa, there were at one time two types of pre-men. One was a great shuffling hulk with a dentition that shows he was a vegetarian. The other was small and active, and fed on flesh as well as vegetable matter. This is the one that can be identified as having a place in the human pedigree. Vegetable gathering produced no tools, no forethought or planning, no tradi-

tion, no social organization. Pre-man the hunter, in developing and using all these for the chase, became man. He became cultured man, and culture grew as he ventured into cold regions, where animal fats and skins were a necessity. Finally, in the flood plains near the desert, he became a farmer. The relation of hunting to the development of cultural traits is expounded by Müller-Using (1951). You may wonder at my use of German references. I wondered myself at the amount of thought and space given to the ethics of hunting by German wildlife biologists and writers, until I remembered that their country still lies under the shadow of the leading antihunting fanatic of modern times, the late Reich Minister of the Interior, Heinrich Himmler. For him, all killing had to be purposeful and humane—gas chambers, not bullets.

There is still another point of view from which hunting and fishing have been pondered, namely, that of the Freudian psychiatrist. Thanks to Professor E. S. Carpenter, of Toronto, I have found one important work, by Menninger (1951), although there may well be more. Freud is another of the great thinkers of our time, and the validity of his early work on dreams and repressions is firmly established. He and his followers often wander beyond the discipline of science, and few concede the complete dominance of sex over the human mind, but because of the element of truth that it contains, the Freudian view must be considered seriously.

According to Menninger, a man who would have no deer killed, and I who kill them, may both be abnormal. The duck hunter who came to his clinic achieved, with the felling of each duck, the destruction of his own mother, for whom, in the slimy pit of his subconscious, and because of some outwardly forgotten chastisement, he had a consuming hatred. I wish that Menninger had gone into the subject of hunters who refuse to eat their game! His duck hunter may have been subject to just such a subconscious drive as he describes, but to imply that all hunters are so is to ignore the most powerful motivation of all. I am sure that hunting appeared to me in my childhood with all its prestige and magic intact, as it was in the beginning. In lands where it has been the prerogative of old families, to whom ancient communities have looked for leadership for centuries, and who can, even in poverty, retain a respect that money cannot buy, its prestige is enormous. I have seen one bedraggled mallard exalt a prosperous immigrant as ranch-style house and Cadillac could never do.

In its broadest sense, we can best express the whole process in terms of play, which Huizinga (1949) shows to be deeply involved in the growth of culture in all its aspects. This all-embracing view of play is not original with him. It is inherent in the very word, which, in its imagery, is seen to include any meaningful activity that goes beyond simple physical need. It was in the play of words that abstractions developed, and many of these had their origin in the chase. Once man became an abstract thinker, the world of make-believe shielded, and assimilated, the serious business of life, which, in the most primitive economies, was largely the chase, so that the divine games of magic, ritual, religion, and law took their place on the stage of human life. Even when it was still necessary, hunting became a game to be played according to the rules, and man would sooner fail in his hunt than succeed by breaking the magic circle. In all this he never lost his place as a part of nature, and to maintain the old relationship is surely not a reversion.

I once called hunting an aesthetic pursuit, but I realize that if one restricts aesthetics to contemplation, as did Baumgarten (1735, 1739), the inventor of the term, then few even of the nonhunting naturalists can qualify as aesthetes. In the broader Socratic sense that assimilates the beautiful to the good and the useful, there could be such a thing as an aesthetic "pursuit," and the chase would certainly be an example. It may simply be enough to say that hunting is a form of play. It can, on occasion, be solemn, or serious, and it can be as exhausting and painful to the participant as the pancratium of the Greek games.

Müller-Using (*op. cit.*) points out that joy in hunting comes before hunting for joy. We find, though, that it is never a simple activity. The assimilation of play to real life is seen in the hunting play of carnivorous animals, but even the kittens on our hearth are ludicrously (the word comes from play) serious in their stalking and leaping, and may bite hard. We cannot, of course, impute cruelty to animals because we have not yet penetrated their minds to find out the quality of their intentions, and thus cannot apply the doctrine of *mens re* to their acts. However, the historian Froude's sometimes quoted "Wild animals never kill for sport: Man is the only one to whom the torture and death of his fellow creatures is amusing in itself," is matched in its unreality and apartness from nature only by Isaac Watts' (1777) "Birds in their little nests agree." Froude (1888) wrote much more eloquently in praise of hunting and fishing. The Russian word for hunt, *okhotit'sya,* which means something done willingly, goes to the root of the matter, and comes out right at the basic definition of play.

That hunting gives satisfaction is inherent in the play definition. The satisfaction is partly aesthetic but it goes much deeper, in that it is rooted in the maintenance by man of an old and harmonious relationship with nature, for wildlife is as truly his prey as it is that of any other predator. Furthermore, the role of the predator, including man, is still vital in the harmonious functioning of the natural community. Something has to happen to the fecund grass-eating masses that Elton (1927) has called the key industries of nature's economy. The face of nature is so altered by man now that feral predators often find little room. The hunter becomes the alternate of disease and starvation.

So we have finished, I hope, with the question of death, and I can see no blame in the hunter, so long as his conscience, ruled by respect for nature, governs his actions. This respect is an emotion, and it must be admitted that the true climax of the hunt is, for most hunting, death. Personally I feel the same way about killing game as I do about felling a tree. The axe is still a symbol, with us; its skillful use carries prestige, and its ring on a trunk brings fulfillment both of a craft and a tradition. Were it used wantonly or wastefully, there would be guilt. The culmination is the cry of "Timber!" even though the pieces may contribute to art and industry in the four corners of the earth.

We still have to consider cruelty, as apart from death. Cruelty, or the willful infliction of pain, is no part of the purpose of hunting. As Lewis (1952) says, cruelty is either the act of a pathological pervert (whom one can pity, and wish cured), or, most reprehensibly, is done for some advantage. As no gain could possibly result from cruelty in hunting, cruel hunters must be perverts. The capacity for such perversion is innate in every human. I have often wondered if some antihunting fanatics, with an extreme preoccupation with the sufferings of animals, are not actually taking their cruelty vicariously. It is, of course, self-evident that there must be pervert hunters, and even fishermen, just as there are pervert clergymen, or boilermakers. No group is exempt, in spite of Xenophon, and we have to watch out for the pervert who deliberately takes up hunting. Primitive man knew and feared such persons, as likely to bring disaster on the tribe by offending the spirits of the animals hunted. When I was north, which is getting to be quite a while ago, there was still living an Eskimo who had been blinded deliberately by his people for just such a reason.

We come finally to the question of the incidental infliction of pain in hunting. In the chase, in the true sense of the word, with dogs, the natural predator is duplicated, and many observations indicate that Nature spares her children fear and pain under such circumstances. David Livingston (1858) remarked on this, after having been himself in the lion's jaws. A hunter who deliberately, ignorantly, thoughtlessly, or through lack of skill which an ethical sportsman would strive for, needlessly risks inflicting pain, is unethical and imperils his moral right to hunt. In shooting, the goal

is a clean kill; if it is not achieved, there remains the knowledge that the death of the same animal in toothless old age would not be less painful. Man, who has the power to determine, in illness and injury, whether the death of his fellow-man is inevitable, refuses to sanction release. He bases his scruples on the very intelligence, which is the source of the fear and apprehension that make the process of death formidable. The starving cow, which even Doctor Schweitzer would permit us to kill, may fear man, whose blows she has felt, or the tiger, whose smell has terrified her kind for millenia, but not the abstract, death. It would be possible to list many things in addition to hunting that bring injury and death to animals, but it would be pointless, because we merely end with a knowledge of the inevitability and infinite variety of death itself, without which there is no life. Hunting remains, as it was in the beginning, completely assimilated to the basic processes of organic nature, in which death and life spring from each other.

It is because of this that hunting is still a life-giving, wholesome sport. Play, whether in ritual, law, religion, games, or any other of its manifestations can lose its roots and become degenerate. Hunting could lose its roots, too. Those who love it must clarify their own ideas as best they can, and become eternally vigilant, especially as the most artificial aspects of human culture spread like a cancer. Above all, we should esteem in ourselves and in our companions that maturity of spirit which alone places the right to hunt beyond question.

In the fantastic mass participation described at the beginning, we see some danger and some good. It is no good trying to make one of the basic activities of the human race on almost all land the exclusive property of a small cult. We have to let them hunt, even though we thereby include those who debase sport. They are the few. Of the rest, we must agree that few have the knowledge or perception to fit into nature as a hunter should. They are, however, willing and eager to learn, conscious of limitations to their own fulfillment imposed by their ignorance. By helping them we help ourselves, the game, and the whole world of nature.

LITERATURE CITED

BAUMGARTEN, ALEXANDER GOTTLEIB. 1735. Meditationes philosophicae de nonnullis ad poema pertinentibus.

———. 1739. Aesthetica.

ELIADE, MIRCEA. 1958. Patterns in comparative religion. (Traité d'histoire des religions.) N.Y.: Sheed and Ward.

ELTON, CHARLES. 1927. Animal ecology. New York:The Macmillan Co.

FROUDE, J. A. 1888. On the uses of a landed gentry. *In* Short studies on great subjects. London: Longmans-Green.

HEBERER, GERHARD. 1951. Menschwerdung und Jagd. Schriftenreihe der Forstlichen Fakultät der Univ. Göttingen, Bd. 2; Vorträge der Hochschulwoche Hann. Münden, pp.12–16.

HUIZINGA, JOHAN. 1949. Homo Ludens, a study of the play element in culture. London: Routledge and Kegan Paul.

LEOPOLD, ALDO. 1938. Conservation esthetic. Bird-Lore, 40(2):101–109.

———. 1947. The ecological conscience. Bull. Garden Club of Amer., Sept. 1947, pp. 46–53.

LEWIS, C. S. 1940. The problem of pain. London:Bles.

———. 1952. Mere Christianity. London:Collins.

LIVINGSTON, DAVID. 1858. Missionary travels and researches in South Africa. New York: Harper.

MCAREE, J. V. 1951. They call it sport. *In* Prose for senior students, an anthology of short stories and essays; selected and edited by J. L. Gill and L. H. Newell, pp. 342–347. Toronto:D. Macmillan and Co. of Canada, Ltd.

MENNINGER, KARL A. 1951. Totemic aspects of contemporary attitudes toward animals. *In* Psychoanalysis and culture, essays in honor of Géza Roheim, pp. 42–72. New York:Int. Universities Press.

MÜLLER-USING, D. 1951. Kultur und Jagd. Schriftenreihe der Forstlichen Fakultät der Univ. Göttingen, Bd. 2; Vorträge der Hochschulwoche Hann. Münden, pp. 35–39.

RUSSELL, MRS. C. E. B. 1941. The path to reconstruction, a brief introduction to Albert Schweitzer's philosophy of civilization. London:Black.

SCHWEITZER, ALBERT. 1922. On the edge of the primeval forest. (Zwischen Wasser und Urwald.) London:Black.

———. 1923a. The decay and the restoration of civilization. (Verfall und Wiederaufbau der Kultur.) London:Black.

——. 1923b. Civilization and ethics. (Kultur und Ethik.) London: Black.

——. 1936. Indian thought and its development. (Die Weltanschauung der indischen Denken.) London: Hodder and Stoughton.

U.S. FISH AND WILDLIFE SERVICE. 1956. National survey of fishing and hunting, 1955. U.S. Fish and Wildlife Circular 44. 50pp.

Voss, R., ET AL. 1955. Wild und Weidwerk der Welt. Vienna: Marathon.

WATTS, I. 1777. Love between brothers and sisters. *In* Divine songs attempted in easy language for the use of children. London: Buckland.

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A NONCYCLIC RUFFED GROUSE POPULATION NEAR ANN ARBOR, MICHIGAN

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This paper presents the results of a study of population trends of the ruffed grouse (*Bonasa umbellus*) on approximately 100 acres of favorable habitat in southern Michigan. The tract surrounds Mud Lake in Sections 1 and 12, T.1S., R.5E., Washtenaw County (Fig. 1). The successional stages range from floating bog, through tamarack–spruce stages to the midtolerant hardwood forest stages. Except for 1954, quantitative observations were made annually of drumming males from 1939 to 1957 by the intersection method described by Graham (1940), thus providing a reliable indication of any marked fluctuations of grouse numbers that occurred during the period.

This swamp is a relict of favorable grouse habitat that was general in the vicinity of Ann Arbor in primitive times. Similar areas, mostly smaller in size, are spotted over the farms and woodlands in the general locality. Thus, the Mud Lake population is not entirely isolated, and the trends there are probably representative of the locality as a whole. This assumption is supported by observations made from time to time in other places.

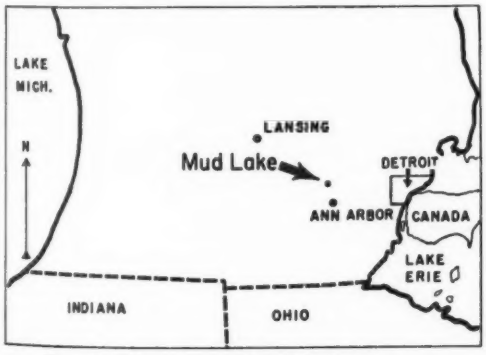

FIG. 1. Location of Mud Lake Swamp.

Beginning in 1927, general observations of the grouse population were made incidentally while conducting other investigations in the swamp. Using bird dogs trained for censusing pheasants, grouse were frequently flushed. Although no detailed records were kept of grouse numbers, it was evident by the mid-1930's that the population trends from year to year did not follow the fluctuations characteristic of more northern localities. During this period a widespread peak in 1932 and a low in 1936 occurred in the northern two-thirds of Michigan (Vollmar, 1952), but no obvious differences occurred at Mud Lake. This situation prompted the initiation of a spring census of drumming males in 1939 in order to obtain more precise information concerning the variations.

HISTORY AND DESCRIPTION

Although the swamp has always been wild land, it has been subjected to a long series of disturbances that have interrupted or modified the classical successional sequences (Fig. 2). Fire, cutting operations, and wind throw are some of these. The classical sequence during the tree stage would be from tamarack (*Larix laricina*) and black spruce (*Picea mariana*) to yellow

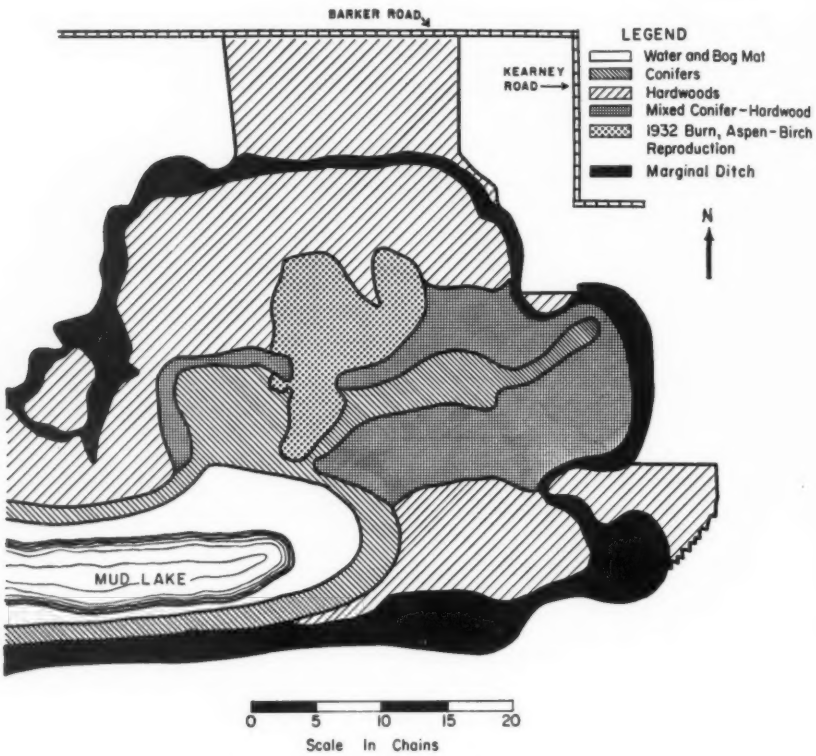

FIG. 2. Mud Lake cover types.

birch (*Betula lutea*), red maple (*Acer rubrum*), and swamp white oak (*Quercus bicolor*). Later, still more tolerant species, such as basswood (*Tilia americana*) and hard maple (*Acer saccharum*) would be expected. However, at Mud Lake, where fire occurred during the coniferous stage, the burned area was promptly invaded by aspen (*Populus tremuloides*), usually in combination with yellow birch. In contrast, cuttings and windfalls have been invaded by various swamp shrubs, especially poison sumac (*Rhus vernix*). Later, these shrubs have been replaced by red maple and in some places by elm (*Ulmus americana*; *U. rubra*). As a result of these disturbances, a great variety of conditions has developed, so that a grouse now finds its every requirement provided for within the swamp.

In 1927 the effects of previous fires were indicated by the presence of several areas of mature aspen. These have today been replaced by red maple, elm, and some yellow birch. The most recent disturbances were a fire in 1932, which destroyed most of the tamaracks on approximately 11 acres in the central part of the swamp, a clear-cut logging operation in 1946 and 1947 that removed trees from about 3 acres in the northern part of the swamp, and another cutting that removed about 8 acres of a fine upland hardwood stand immediately north of the margin. The reduction in the amount of suitable nesting cover brought about by (a) these logging operations and (b) the disappearance of mature aspen through successional changes is sufficient to explain a downward trend of the grouse population. But, still other changes have been potentially deleterious. For example, ascendancy of the midtolerant hardwoods has suppressed and eliminated much poison sumac and huckleberry (*Gaylussacia baccata*), both excellent grouse foods. In the burned part, aspen and yellow birch have replaced the tamarack and black spruce, but they have shown exceptionally slow growth and considerable defect and mortality. Both of

these species may ultimately be useful to the grouse if they reach a stage when flower buds are produced in abundance. Thus far, however, grouse have used the burned area to a relatively small extent. The older parts of the swamp comprise approximately 50 per cent of the area, and it is there that the grouse are concentrated.

Surrounding the swamp are croplands and pastures interspersed with small woodlands, usually grazed. These lands are not attractive to grouse, although the wood lots may be used sporadically. Several small, wooded kettle-hole swamps are within ½ mile of Mud Lake, but they are not large enough to support a permanent grouse population. Thus, Mud Lake Swamp is an island of good habitat surrounded by less favorable conditions within several miles. Some hunting was done each year until 1957, when the land was acquired by the University of Michigan and established as an inviolate natural area.

POPULATION CONTRASTS BETWEEN MUD LAKE AND NORTHERN MICHIGAN

After 18 years of drumming records, the relative stability of the grouse population in Mud Lake Swamp is clearly demonstrated. Widespread depressions of the grouse population occurred in the northern two-thirds of Michigan about 1945 and again about 1955, whereas peaks occurred about 1940–41 and 1951–52 (Vollmar, *ibid.*;

TABLE 1.—RUFFED GROUSE POPULATION FLUCTUATIONS IN MICHIGAN (Leopold, 1931; Tubbs, 1940; Mich. Biennial Reports)[1]

Year	Period of Maximum Abundance	Period of Decreasing Abundance	Period of Scarcity	Period of Increasing Abundance
1880	X			
1886			X	
1891	X			
1895			X	
1896–1900				X
1901	X			
1902–04		X		
1905–06			X	
1907–09				X
1910	X			
1911–14		X		
1915–16			X	
1917–19				X
1920–21	X			
1922–24		X		
1925–26			X	
1927–29				X
1930–31	X U.P.[2]			
1932	X U.P.			
1933–35		X		
1936			X	
1937–40				X
1941–42	X			
1943–44		X		
1945			X	
1946–50				X
1951–52	X			
1953–54		X		
1955			X	
1956–?				X

[1] Extended from Vollmar, 1952. [2] Upper Peninsula of Michigan.

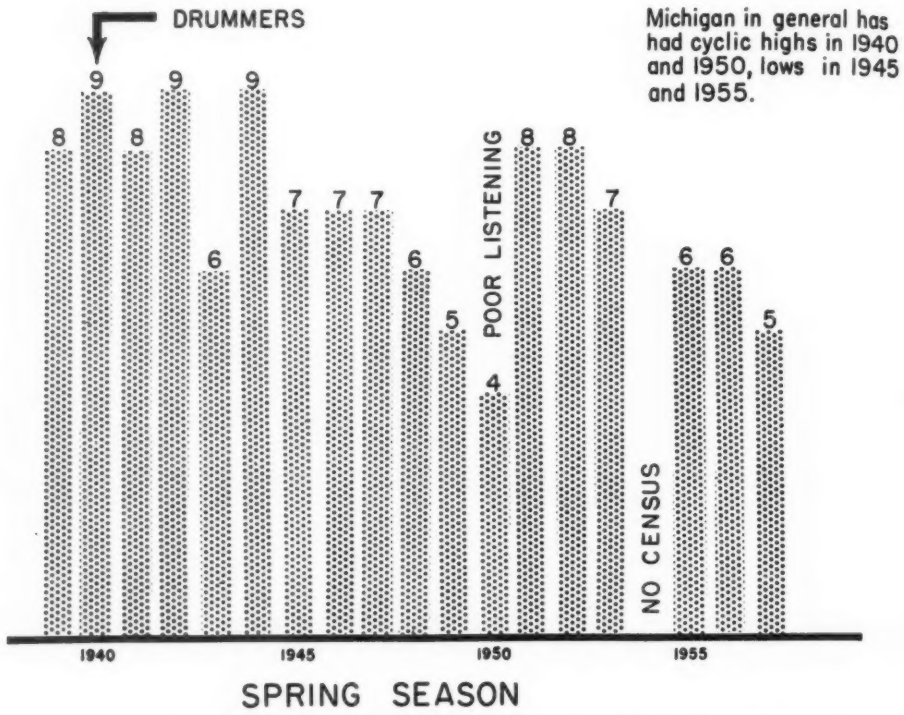

FIG. 3. Number of drumming grouse males at Mud Lake during spring.

Shapton, 1955). Table 1 summarizes the general population trends for northern Michigan.

Fig. 3 illustrates the number of grouse drumming each year at Mud Lake from 1939 to 1957, inclusive. The record for 1954 is missing, and the count in 1950 is undoubtedly low because windy weather interfered with hearing. Any error that has crept into these data will certainly be on the conservative side, since only birds heard with certainty were recorded. Graham (*op. cit.*) has described and discussed in detail the method of censusing grouse used in this report.

If it is assumed that the sexes occur in equal numbers, the Mud Lake grouse population has fluctuated between 10 and 18 birds per 100 acres. During the same period in other localities in the Lower Peninsula of Michigan, the population per 100 acres varied as follows, according to Fisher (1939) and Palmer (1956):

Northern Lower Peninsula	max. 6.6	min. 0.5
Central Lower Peninsula	max. 11.0	min. 3.1

The divergence from the average population was less than 30 per cent at Mud Lake, 57 per cent in central Michigan, and 86 per cent in the northern Lower Peninsula. The relatively minor fluctuations at Mud Lake were unrelated to the peaks and depressions that have occurred in the other parts of the state, mentioned above.

During the past 12 years, several graduate students conducted intensive studies of the grouse at Mud Lake. Leebrick's (1946) work included flushing observations during the winter of 1945–46. The first half of his study was made without a dog, but during the late winter and spring a cocker spaniel was used to flush the birds. He estimated the grouse population at 10 to 14 birds. The drumming-male count in the spring of 1946 was 7 which, when doubled, agrees closely with Leebrick's findings.

Aided by a dog in making counts, Wilson (1948) estimated that 20 grouse were present at Mud Lake early in 1947. Re-examination of his actual flushing data suggests that this is too high a figure. Also, three birds

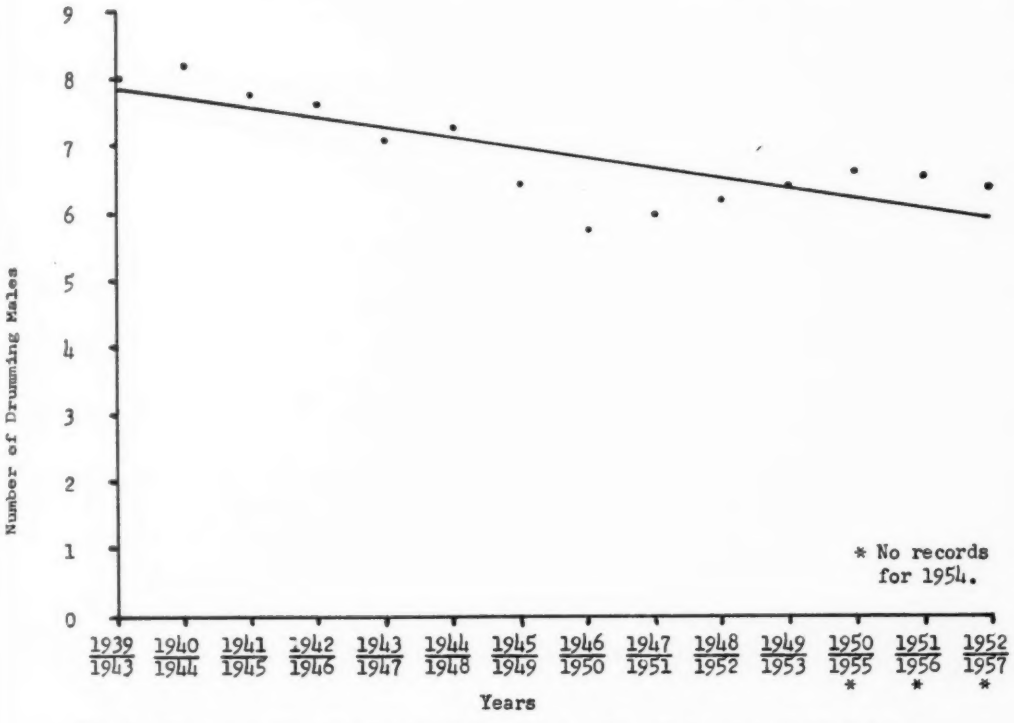

FIG. 4. Five-year running average of drumming male ruffed grouse at Mud Lake.

were known to have been killed by predators prior to the drumming census in the spring of 1947. The spring count indicated a population of 14 birds (7 males). Therefore, the results of the two methods of census are reasonably consistent.

Wilson estimated that 18 grouse were present in December 1947. The drumming count 4 months later indicated 12 grouse (6 males) at Mud Lake. Considering possible winter losses, the spring census appears to be reliable.

Wenzel (1956) estimated that 11 grouse were in the swamp during the winter of 1952–53. The drumming count of 7 males would place the spring population in 1953 at 14 birds. There is satisfactory agreement between the results when one considers that Wenzel's estimates could well have been low, since he used no dog. In short, the populations derived from the spring drumming censuses appear to correspond with the more intensive work of Leebrick, Wilson, and Wenzel.

POPULATION TRENDS

Ruffed grouse population trends at Mud Lake have coincided neither temporally nor in magnitude with the general fluctuations occurring in northern Michigan for some 30 years. Neither the earlier nonquantitative observations nor the more exact drumming counts indicate a cyclic trend.

Mud Lake grouse numbers remained essentially constant during the northern Michigan period of decline between 1943 and 1945 and decreased somewhat during the following rise in the north. More recently, the birds in Mud Lake Swamp decreased somewhat during the northern Michigan slump that followed the 1952 peak. No upward swing at Mud Lake has occurred, although the northern population is approaching another peak.

As stated previously, the divergence from the average grouse numbers at Mud Lake has been less than 30 per cent. Leopold (1933) defines a cyclic population as one that fluctuates at least 50 per cent from

the average. In the northern two-thirds of Michigan the magnitude has been greater than Leopold's minimum.

Although there has been no evidence of cyclic fluctuation, there has been a general decline in grouse numbers since 1939. A 5-year running average of the spring populations indicates clearly a decline explainable, as has been pointed out, by changes in food and cover conditions on the study area (Fig. 4).

There appear to be five reasons explaining the relative stability of grouse numbers at Mud Lake. (1) The amplitude of population fluctuations of many animals is characteristically less from the poles toward the equator. (2) Also, the amplitude is likely to be less in localities where an animal is close to the center of its original optimum range, which for the ruffed grouse is not far south of Ann Arbor, according to Leopold (1931:149; 1933: 59–61). (3) Because of its relative isolation, the Mud Lake Swamp might not be subject to the biotic causes that may initiate grouse fluctuations elsewhere. (4) Without such influences the relatively good food and cover conditions within the swamp would be conducive to a steady population. (5) Certainly the so-called cycles are associated with large continuous blocks of range, as distinguished from small discontinuous ones, according to Leopold. Therefore, Mud Lake would be a logical place to find a stable population. But, whatever the reasons, the fact is clear that during a period of over 30 years the grouse population at Mud Lake has shown no evidence of cyclic fluctuation.

SUMMARY

The ruffed grouse population in Mud Lake Swamp in southern Michigan has been studied from 1927 to 1957. The swamp has remained in a wild condition and has supported grouse year after year. The first 12 years of study were observational in nature, but more intensive research was begun in 1939 in the form of a drumming-male census.

The relative stability of the population at Mud Lake is clearly demonstrated. Divergence from the average population in the swamp has been much less than that reported for the northern two-thirds of Michigan. Natural succession, logging, and fire have caused habitat changes and a gradual reduction in grouse numbers in the past 18 years.

REFERENCES CITED

FERNALD, M. L. 1950. Gray's manual of botany. Eighth edition. N.Y.:American Book Co. v+1632pp.

FISHER, LEE WLLIAM. 1939. Studies of the eastern ruffed grouse (*Bonasa umbellus umbellus*) in Michigan. Mich. State College, Agric. Exp. Sta., Tech. Bull. No. 166. 46pp.

GRAHAM, SAMUEL A. 1940. The intersection method of counting animals. J. Wildl. Mgmt., 4(3):313–314.

LEEBRICK, KARL CLAYTON, JR. 1946. Ruffed grouse in the tamarack–hardwood associations of southern Michigan. Unpubl. Master's thesis, Univ. of Mich., Ann Arbor. 82pp.

LEOPOLD, ALDO. 1931. Report on a game survey of the North Central States. Madison, Wis.: Sporting Arms and Ammunition Manufacturers' Institute. 299pp.

———. 1933. Game management. N.Y.:Charles Scribner's Sons. xxi+481pp.

MICHIGAN DEPARTMENT OF CONSERVATION. 1922. Biennial Report. No. 1. 358pp.

———. 1924. Biennial Report. No. 2. 307pp.

———. 1928. Biennial Report. No. 4. 303pp.

———. 1932. Biennial Report. No. 6. 205pp.

———. 1934. Biennial Report. No. 7. 224pp.

———. 1936. Biennial Report. No. 8. 264pp.

———. 1938. Biennial Report. No. 9. 315pp.

———. 1940. Biennial Report. No. 10. 331pp.

———. 1942. Biennial Report. No. 11. 326pp.

———. 1946. Biennial Report. No. 13. 321pp.

———. 1950. Biennial Report. No. 15. 351pp.

PALMER, WALTER L. 1956. Ruffed grouse population studies on hunted and unhunted areas. Trans. N. Amer. Wildl. Conf., 21:338–345.

SHAPTON, WARREN. 1955. Down but not out. Mich. Cons., 24(5):3–6.

TUBBS, F. F. 1940. Grouse cycles. Mich. Cons., 9(12):2,10.

VOLLMAR, BRUCE F., JR. 1952. History of the ruffed grouse, *Bonasa umbellus*, in Michigan. Unpubl. Master's thesis, Univ. of Mich., Ann Arbor. 84pp.

WENZEL, DUAINE K. 1956. A comparative study of ruffed grouse, *Bonasa umbellus* L., in Washtenaw County, Michigan. Unpubl. Master's thesis, Univ. of Mich., Ann Arbor. 50pp.

WILSON, HERRICK LEE. 1948. The effect of topography and land use on ruffed grouse in southern Michigan. Unpubl. Master's thesis, Univ. of Mich., Ann Arbor. 97pp.

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BRIEFER ARTICLES

CONSUMPTION OF ALFALFA AND WILD OATS BY *MICROTUS CALIFORNICUS*

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To obtain some measure of the economic effect of field mice or voles (*Microtus californicus*) on agricultural land, tests were run to determine the forage intake of captive individuals. The destructiveness of field mice on grasslands and in alfalfa fields is more or less proportionate to the amount of forage they cut from the plants. Some of that which they cut is eaten, and the balance is left on the ground to dry, and all of this is lost from agricultural production. Although the amounts consumed by captive individuals may not be the same as those of free-living individuals, the laboratory-derived data can provide a rough index of the economic effect of a wild population. Computations of this sort are open to criticism, but they have value until a superior method is proposed. Plant growth on areas from which mice are excluded would serve as a check on the following trials; but wire exclosures may introduce environmental changes and are not sufficient, by themselves, in ascertaining forage use of field mice.

Methods

The mice used in the following trials were trapped in Sutter County, California, and on geographical grounds were *Microtus californicus aestuarinus*. Each mouse was kept in a separate cage, the bottom of which was hardware cloth so that the uneaten food could easily be recovered from the tray underneath. These cages were in a laboratory, at temperatures of 60°–70°F. Drinking water was not available.

The mice were fed weighed amounts of fresh alfalfa (*Medicago sativa*) and wild oats (*Avena fatua*). These tests were made in April, and the plants were growing and green at that time. Samples of these plants were oven dried and weighed to determine the dry weight for a given amount of green food. The alfalfa contained 75 per cent water and the wild oats 80 per cent water. Each morning the uneaten food was dried and weighed; this weight subtracted from the dry weight of the food offered on the previous day indicated the dry weight eaten by the mouse.

Sixteen nongravid adult females were divided into two groups of eight, each group with a mean weight of 45 grams. One group was fed fresh alfalfa for five days, while the second group was given fresh wild oats. The diets were then reversed and the feeding trials repeated, so that each mouse had been offered both plants for five days. Sixty grams of fresh food were offered daily to each individual; and the food intake calculated in terms of fresh weight, dry weight, and daily weight consumed in relation to the weight of the mouse.

Results of Feeding Trials

Throughout the period during which the mice were fed known quantities of fresh forage, the mean weight of the animals in each group remained 45 grams. As the amounts of fresh alfalfa and wild oats eaten (Table 1) are so nearly identical, it appears that animals fill themselves to capacity, the difference in the dry weight intake reflecting the difference in water content of the two plants. In captivity, this species eats about 85 per cent of its body weight in fresh food daily.

In the field, *Microtus* characteristically cuts a tall stem of alfalfa and then strips it of its tender leaves; in the laboratory, the mice fed in the same way, clipping the leaves and avoiding the fibrous stems. The leaves and stem on an alfalfa plant are approximately equal in dry weight. The mice ate heads and tender parts of the blades of wild oats, and tended to reject the more coarse parts of the culms.

Discussion

Economic justification for limiting the numbers of a wild animal rests on the relationship of two

Table 1.—Consumption of Alfalfa and Wild Oats by Captive *Microtus californicus*
All weights in grams

Food	Number of Mice	Mean Weight[1] (gm.)	Fresh Weight of Food[2] (gm.)	Dry Weight of Food[2] (gm.)	Food Eaten as Percentage of Mouse Weight	
					Fresh	Dry
Alfalfa	16	45	39	9.8	87	22
Wild oats	16	45	38	7.6	85	17

[1] No change in weight over 5-day periods.
[2] Mean daily weight eaten, per individual.

pieces of information: the cost and effectiveness of controlling a given species, and the extent of the damage done by that species. Too often this relationship is not evaluated; the decision to destroy economically harmful animals is frequently made without an estimation of the expense and the possible benefits.

By converting the data on the use of food by laboratory mice, one may derive an approximation of the damage these rodents inflict upon forage crops. In appraising these estimates, one should realize that unknown variables detract from their validity. Wild mice may eat more or less than captives, and the amount eaten is not the same as the amount destroyed. Also important is the unknown density of mice, which may increase or decrease from spring to autumn. However, one may attempt to establish the economic loss of a hypothetical population of field mice.

A series of complaints of *Microtus* damage in the Sacramento Valley and Delta concerned populations that ranged from 60 to 135 mice per acre. These densities were calculated by the modification of the Lincoln Index proposed by Hayne (1949). A population of 100 mice per acre is sufficient to attract the rancher's attention and can cause appreciable economic loss. The damage done by such a density can be calculated; figures one-half and one and one-half times this amount will approximate the losses where mice are 50 per acre or 150 per acre, respectively.

One mouse consumes about 10 grams of dry alfalfa daily, or about 300 grams per month; this figure is for a mouse weighing 45 grams, similar to the mean weight in a heterogeneous population. Thus, a population of 100 field mice per acre will eat 30 kilograms of dry alfalfa per acre per month, or about 210 kilograms (or 462 pounds) during a 7-month growing season. This amount does not represent the final loss to the farmer, for the mice eat only the leaves, and destroy an equal weight of stems. Accordingly, these mice would destroy about 924 pounds of dry alfalfa per acre during a 7-month growing season. Populations of 50 and 150 mice per acre would destroy 462 and 1,386 pounds, respectively. Knowing his annual production of alfalfa, a farmer may obtain at least a crude idea of the percentage of forage removed by these rodents. In the Sacramento Valley a typical harvest of alfalfa on 2- and 3-year-old stands is about 22,000 pounds per acre per 7-month season. One hundred mice per acre could account for 4 per cent of the annual crop; or densities of 50 and 150 mice would take 2 and 6 per cent, respectively. In fields where weeds are controlled, the field mice subsist almost solely on alfalfa, and the above calculations are probably of practical reliability.

In conventional control of field mice, using 1 per cent zinc phosphide on rolled barley, the kill may be between 90 and 95 per cent with initial populations of 75 to 135 *Microtus* per acre (Jameson, 1958). When poisoning field mice, the rancher may calculate the expense of control and estimate the possible benefit (crop protection) to be derived from such control.

An hypothetical example may illustrate the relationship between cost of control and damage by mice. Currently the cost of the prepared poisoned bait is about 6.3 cents per pound; applying 5 pounds of bait per acre, the farmer's materials cost him about 31.5 cents per acre. This is sufficient bait for mouse populations of from 50 to 150 per acre. Distribution of the bait by hand is generally the most expensive method, and costs approximately $1.04 per acre at present farm labor wages of $1.25 per hour. One man can distribute bait on about 10 acres in 8 hours. The total cost of poisoning *Microtus* by this method is $1.35 per acre. In the Sacramento and San Joaquin valleys, good alfalfa production is about 11 tons per acre per season; and at the current price of $25 a ton, the alfalfa from one acre is worth about $275 a season. The estimated loss to field mice is from 462 to 1,386 pounds, or from $5.50 to $16.50 per acre for populations of 50 and 150 mice per acre, respectively. With a removal of 90 per cent of these mice by poisoning, the loss should be reduced proportionately. Because field mice occasionally reproduce rapidly, poisoning may be necessary several times a season if their numbers are to be kept low.

In many regions in the western United States, sheep and *Microtus* exist on the same pastures, and compete for much of the same food. Sheep are important pasture animals in parts of the Sacramento–San Joaquin Delta, the heaviest summer lamb feeding area in California; and here field mice are often common. The typical weight of lambs on these pastures is about 39 kilograms or 86 pounds, and the dry weight food intake is about 1,400 grams or 3.1 pounds daily. At the height of the growing season, there are about ten lambs per acre of irrigated pasture, and they will take about 14 kilograms or 31 pounds of forage every day. Here, the available forage consists of several kinds of plants, and the amount eaten by field mice in a pasture can be estimated from their consumption of wild oats and alfalfa in the laboratory. One hundred mice should take 1 kilogram of alfalfa or 760 grams of wild oats daily; other more palatable pasture grasses are probably eaten at a rate between these two figures. One may assume that 100 field mice eat 880 grams of pasture forage and, in feeding, destroy an equal weight, bringing the total to 1.76 kilograms (dry weight) per day per acre. Thus, on an irrigated pasture, 100 field mice per acre take about 12 or 13 per cent as much forage as the lambs; 50 and 150 would take 6 and 18 per cent, respectively, of the amount taken by ten lambs. These pastures are usually stocked to capacity, and a large population of field mice (between 50 and 150 per acre) would destroy sufficient forage to force the rancher to provide additional food for the lambs. A heavy density of field mice on pasture lands can thus be a serious threat to the rancher's

investment, and the cost of poisoning mice is much less than the possible alternate necessity of supplemental feeding.

SUMMARY

Captive field mice ate 9.8 grams of alfalfa and 7.6 grams of wild oats, dry weight, daily. On an acre of sheep pasture, 100 mice will consume 12 to 13 per cent as much forage as ten growing lambs. In an alfalfa field with this density of mice, they will destroy about 4 per cent of the annual production.

LITERATURE CITED

HAYNE, DON W. 1949. Two methods for estimating population from trapping records. J. Mammal., 30: 399–411.

JAMESON, E. W., JR. 1958. The cost and effectiveness of controlling *Microtus* by zinc phosphide. J. Wildl. Mgmt., 22:100–103.

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AN EFFECTIVE REPELLENT FOR EUROPEAN HARE IN BRAZIL[1]

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This paper reports some observations of damage to young deciduous fruit trees by hares in southern Brazil, as well as some tests that resulted in finding an effective repellent. The work was carried out during a leave of absence from Michigan State University in 1953 and 1954 when I was with the United States Department of Agriculture, Foreign Agricultural Service, in the "Point 4" technical aid program with the Instituto Agronomico do Sul, Pelotas, Brazil.

CLIMATE

Fernando S. da Mota (1950) has reported on 56 years of weather records (1893–1948). From his studies the following items are taken. Pelotas is situated at 7 meters of altitude (23 feet), lat. 31°45'S., long 52°21'W. The annual mean temperature (1893–1948) has been 18.2° C. (64.8° F.) and the average precipitation 1282.9 mm. (50.5 in.).

Using the climatic classifications of Koeppen, Thornthwaite, Setzer and Knocke, Mota (*ibid.*) concludes that the climate of Pelotas should be classified as of a temperate zone. July is the coldest month, February the hottest, September the rainiest, November with the least rain, June the most humid, and November the driest.

INJURY FROM EUROPEAN HARE

At the Central Experiment Station of the Institute, the Chief of the Station, Eduardo C. Gomes, called my attention to the severe injury to young fruit trees (Fig. 1) from feeding of the European hare. The animal was identified as *Lepus europaeus* by the staff of the museum of the school. The trees were 1 to 4 years old, the result of much replanting. The planting comprised 108 apple trees, 126 plum trees, and 119 pear trees, with varieties as listed in Table 1.

In 1953, during May and the end of autumn in Brazil, a survey of the planting showed that 62 per cent of the apple trees, 24 per cent of the plum trees, and 66 per cent of the pear trees had been injured by the feeding of hares. Of the 353 trees, 175 were thus injured.

FIG. 1. An apple tree showing typical injury from feeding by European hare in the state of Rio Grande do Sul, Brazil.

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[2] The author desires to express appreciation to Don W. Hayne, Peter I. Tack, George A. Petrides, and Rollin H. Baker for advice in the preparation of this manuscript. Special appreciation is extended to Jose Emilio Goncalves Araujo, Engo. Agro. and Director, Instituto Agronomico do Sul, Pelotas, Brazil, who proposed this study. Acknowledgment goes to the many staff members of that institute for the friendly help given to the author.

TABLE 1.—SPECIES, VARIETIES, AND NUMBER OF TREES INJURED BY HARES

APPLE			PLUM			PEAR		
Variety[1]	Total Trees	Trees Injured	Variety[1]	Total Trees	Trees Injured	Variety[1]	Total Trees	Trees Injured
Stayman	9	5	Giant	9	5	Garber	12	5
Spy	9	2	Burbank	10	3	Duchess	12	10
Starking	10	5	D'Angan[2]	10	4	Kieffer	14	8
Winesap	10	9	Wickson	10	0[3]	Smith	16	11
Mother	10	8	Reine Claude	20	6	LeConte	17	9
Monroe's Favorite	10	7	Kelsey	10	1	P. Crassane	15	12
Jonathan	10	8	Golden Japan	10	4	Wm. Christ	16	13
King David	10	8	Santa Rosa	29	4	D'Agua	17	10
Banana	10	4	The First	9	0[3]			
Rome	10	6						
Delicious	10	5						

[1] Names and spelling as on row stake labels. [2] May be D'Agen or French prune. [3] Trees larger than 5.25 cm. (2 in.).

In recording injury, I estimated the diameter of each tree at 4 inches above the ground (Table 2). Beyond the obvious effect of size (large trunk, less damage), the kind of tree seemed to influence damage. To test this point, the data were pooled (1) for all trees 2.5 cm. (1 in.) and less in diameter, and (2) for trees between 3.25 cm. (1½ in.) and 5.25 cm. (2 in.). In both sets of data, plums were least damaged, and chi-square tests showed the differences among kinds to be significant at the 5 per cent level.

A REPELLENT TRIAL ON APPLE TREES

At the beginning of winter, in June 1953, the first sign of fresh feeding on fruit-tree bark was noted. I was then able to obtain wood rosin and ethyl alcohol to make the type of repellent coating that had proven to repel cottontail rabbits (*Sylvilagus floridanus*) in Michigan (Cardinell, Toenges, and Hayne, 1941). It was prepared by dissolving 3.18 kg. (7 lbs.) of wood rosin in 3.8 liters (4 qts.) of ethyl alcohol. This mixture was painted on alternate trees insofar as possible and so recorded on a map of the planting. Wherever possible, uninjured trees were treated, affording 51 treated trees and 57 untreated controls, the same young apple trees listed in Table 2. Time did not permit assembling other materials that had proven effective in pen tests in Michigan (Cardinell and Hayne, 1947).

Toward the end of winter, on August 16, 1953, all trees were critically examined. None of the trees coated with the rosin alcohol varnish showed any fresh signs of feeding by the hares. The untreated control trees showed that 16 trees had been freshly fed upon.

After one year's weathering of the rosin alcohol coating, the trees were re-examined to see if some degree of repellency persisted, as was observed with the species of rabbit found in Michigan (Cardinell and Hayne, *ibid.*). Only one fresh bite was evident on one of the treated trees the second winter, and considerable fresh feeding was noted again on the untreated trees.

TABLE 2.—PROPORTION OF FRUIT TREES DAMAGED BY EUROPEAN HARE, IN RELATION TO TRUNK DIAMETER AND KIND OF TREE, WITH NUMBERS OF TREES SHOWN IN PARENTHESES

Diameter In.	Diameter Cm.	Apple	Plum	Pear	Totals
½	1.3	0.50(10)	0.67(12)	0.70(10)	0.62(32)
¾	1.9	0.80(20)	0.50 (6)	0.80(30)	0.77(56)
1	2.5	0.68(31)	0.60(10)	1.00(18)	0.76(59)
1¼	3.2	0.88 (8)	0.38 (8)	0.55(20)	0.58(36)
1½	3.8	0.67(18)	0.30(23)	0.30(10)	0.43(51)
1¾	4.4	0.33(12)	0.14(14)	0.50 (8)	0.29(34)
2	5.1	0.44 (9)	0.03(33)	0.42(19)	0.25(61)
2¼	5.7			0.25 (4)	0.25 (4)
2½	6.4		0 (10)		0 (10)
2¾	7.0				
3	7.6		0 (10)		0 (10)
Averages		0.64(108)	0.24(126)	0.64(119)	0.50(353)

SUMMARY

The European hare (*Lepus europaeus*) in the state of Rio Grande do Sul, Brazil, was found to injure the trunks of young trees of apple, plum, and pear. A varnish made of rosin dissolved cold in ethyl alcohol proved to be completely effective when painted on the bark of trunks and low limbs of 51 young apple trees during the winter of 1953. With one exception, it was effective during the following winter of 1954.

LITERATURE CITED

CARDINELL, H. A. AND D. W. HAYNE. 1947. Pen tests of rabbit repellents. Mich. Agric. Exp. Sta., Quart. Bull., 29:303–315.

CARDINELL, H. A., WALTER TOENGES, AND D. W. HAYNE. 1941. A fruit tree coating effective against cottontails. Mich. Agric. Exp. Sta., Quart. Bull., 24:65–68.

MOTA, FERNANDO SILVEIRA DA, 1950. Contribuicao ao estudo do clima de Petotas. Agros [a student publication at Escola de Agronomia, Pelotas, Brazil], 3(3): 134–159.

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A SUMMARY AND RECLASSIFICATION OF BOBWHITE FOODS

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A great many plants are known to furnish food for bobwhite (*Colinus virginianus*). Most of them will respond to some form of agricultural management; but only a few of them are sufficiently useful to bobwhite to justify agricultural effort in their production. For successful management of land and vegetation to benefit bobwhite, therefore, it is important to know the relative value of these food plants. (Plants supply about 85 per cent of the bobwhite's food, the other 15 per cent being animal foods—beetles, bugs, caterpillars, centipedes, crickets, grasshoppers, katydids, leafhoppers, snails, spiders, walkingsticks.)

This paper presents an evaluation of bobwhite food plants as to their quality and acceptance, and classifies them as "choice," "inferior," and "unimportant." This is a departure from conventional classifications, but is similar to the one we have made of deer and turkey foods (Davison and Graetz, 1957).

The range of this paper's applicability has no geographical bounds. Neither is it influenced by seasons nor field conditions. It simply classifies plant foods qualitatively for the species, bobwhite. Any local management plan should, of course, select (from the choice foods) only those that are well adapted to the climate, soils, seasons, managerial desires, and related field conditions. Many previously published classifications determined "preferences" in the light of only locally available sources of food, and failed to weigh the evidences of digestibility, nutrition, and free choice (foremost exceptions: Nestler, *et al.*, 1945; Michael and Beckwith, 1955; Davison, 1940 and 1942). The author has studied the evident "free choice" of foods selected by more than 7,000 bobwhites afield in the southern and central sections of their range during fall, winter, and spring.

The term "choice" refers to a good-quality food —one that is digestible, nutritious, and eaten readily when available. Of course, bobwhites display preference among choice foods; but a choice food of any kind is worthy of consideration in management. The foods listed as choice number 68 species.

Foods that are mediocre in digestibility, nourishment, or acceptability are classed as 'inferior." Failure to differentiate between choice and inferior foods interferes with intelligent management of soils and plants for bobwhite. Occasionally an "inferior" food is worthy of consideration in a specific situation. Some can be improved by fertilization, cultivation, or selection of superior strains. An example is the Soil Conservation Service's development of improved Japonica lespedeza (Davison, 1954). We have listed 70 species as being inferior foods.

A long list of "unimportant" plants includes 378 species and is omitted in this paper. These plants may be eliminated entirely from agricultural consideration for bobwhites.

The foods are listed alphabetically in each grouping by common names, using *Standardized Plant Names* (Kelsey and Dayton, 1942) as the authority. Most published tables list the foods in a descending order according to "volume," "frequency of occurrence," or some combined "index" of the two. These were efforts to show relative "importance" or "preference" among foods in the locality of the study. Few studies have been extensive enough to make such detailed preferences valid.

Most students of bobwhite feeding habits will recognize the validity of the 68 species listed as choice foods; except four o'clock (Denis Hart, *in litt.*, 1953) and rape (Michael and Beckwith, *op. cit.*), which were found to be readily acceptable in pen-feeding experiments. The other 66 have been recorded as being choice foods by numerous authors, in one or more areas where bobwhites live (Stoddard, 1931, Georgia and Florida; Korschgen, 1952, Missouri; Laessle and Frye, 1956, Murray and Frye, 1957, Florida; Lay, 1954, Lehmann and Ward, 1941, Texas; Lee, 1948, Oklahoma; Davison, 1942, Southeastern States; Martin, Zim and Nelson, 1951, Patuxent Laboratory).

At the other extreme are the unimportant foods, which have been found in quail gizzards (and occasionally in craws). If a plant has been found to have been eaten in significant quantity anywhere in the bobwhite's entire range, it cannot be included in this group. There is no evidence to support the frequently mentioned theory that any one of these plant foods may contain a minor element needed in the diet. A few plant foods may have fallen into this "unimportant" category due to their limited availability; but this would be exceptional, since almost every plant in the list is commonly available in one or more of the areas for which bobwhite food studies have been published. Several of these "unimportant" foods (such as sickle senna, rough peavine, chufa, lupines, bermudagrass, and showy crolataria) have been proven to be unacceptable, and some even toxic, in feeding experiments (Stoddard, *op. cit.;* Nestler, *et al.*, *op. cit.;* Michael and Beckwith, *op. cit.*). In addition, as shown by Davison (1940, 1942), hard-seeded plant foods (such as buttonweed, grape, greenbrier, hackberry, native perennial lespedezas, sericea lespedeza, poisonivy, rose, and the sumacs) occur commonly in bobwhite gizzards, where they are virtually in-

digestible, but they do not occur in the craw in significant quantities. Failure to find commonly in the craws such abundant seeds as silktree albizzia, amorphas, black cherry, clover seeds, coralberry, crabgrass, dallisgrass, dock, hawthorn, honeysuckle, indigo, giant ragweed, redbud, redcedar, rosinweeds, Russianthistle, smartweeds, yaupon, and many others seems to be sufficient justification to call them unimportant.

One may more properly question the author's decisions that placed each of 70 species in the class of "inferior." Each of them has been found in a few or many bobwhite craws, in sufficient quantity to indicate some significance. Yet, in light of availability in the field, most of these foods would show up more abundantly in bobwhite craws if they were "choice." Other considerations were (with examples): (1) poor digestibility (southern waxmyrtle, which is found in large quantity in craws and gizzards in coastal areas); (2) apparent bitter or acrid taste (bumelia, inkberry, black locust, sesbania, stillingia). Some of the "inferior" plants might have deserved the "choice" rating if they had been more abundantly available (beech, buckwheat, butterfly pea, two crotons, hogpeanut, osageorange, panic grasses, persea, rhynchosia, rushfoils, sassafras, treadsoftly, and wild beans). More summer studies might lift blueberry, carpetgrass, oat, and raspberry to the choice classification. Feeding experiments might prove some of these plants to be worthy of the term "choice." From the author's extensive studies and the literature to date, however, the decisions could scarcely be otherwise than to list them as being "inferior."

This evaluation does not prescribe management practices. It is a step between research and management. It has been useful as a reference guide in the preparation of management instructions for farms, and local and regional areas. It may point up needed research.

Similar evaluations of plants for other American birds are being made, and manuscripts are now in preparation. Therefore, the author will appreciate suggestions regarding this classification of bobwhite foods and any corrections needed in the placement of each plant species as "choice" and "inferior" in bobwhite diets.

CLASSIFICATION OF BOBWHITE PLANT FOODS

CHOICE: bean (mung); blackberry; browntop-millet; clover (crimson, white); corn; cowpeas; croton (linear, punctate, Texas, woolly); dogwood (flowering); four o'clock; lespedeza (bicolor, common, Kobe, Korean, Japan, Thunberg); milkpea (erect, hoary); oak acorns (live, lowbush, pin, post, southern red, water, willow); panicum (browntop, fusiform, Texas); partridge pea (sensitive, showy); paspalum (barestem, bull); peanut; pearlmillet; pecan; pine (loblolly, longleaf, pitch, shortleaf, slash, spruce, Virginia); ragweed (blood, common, lanceleaf, western); rape; razorsedge (fringed, sloughgrass); rice; rye; sesame; sorghum (grain); strawberry; sunflower (common); sweetgum; switchgrass; tickclover (beggarweed, diamondleaf, Dillen, panicled); vetch (hairy, narrowleaf); wheat; wildbean (pink).

INFERIOR: amaranth (prostrate, redroot, spiny); ash; bayberry (northern); beech (American); blackgum; bladderwort (awn); blueberry (ground); buckwheat (common); bumelia (woollybucket); butterflypea (coastal); carpetgrass (big, common, tropical); clover (alyce); clusterpea (Boykin); croton (oneseed, tropic); hogpeanut (southern); goldstargrass; gopherapple; inkberry; Johnsongrass; locust (black); lovevine; mentzellia; oat; osageorange; palmetto (cabbage); panicum (beaked, bicknell, *clandestinum*, dominican, fall, flexile, longleaf, needleleaf, *neuranthum*, *oligosanthes*, proso, roundseed, Tennessee, velvet, warty, woolly); paspalum (Florida); persea (redbay, swampbay); prairieclover (September); potatobean; puffballfungus; raspberry (red); rhynchosia (dollarleaf, erect); rushfoil (twofruit, linear); sassafras (common, silky); sesbania; skunkcabbage; snapweed; stillingia (corkwood, dentate, queensdelight); sudangrass; treadsoftly (risky); waxmyrtle (southern); wildbean (small, trailing).

REFERENCES

DAVISON, V. E. 1940. A field method of analyzing game bird foods. J. Wildl. Mgmt., 4(2):105–116.

———. 1942. Bobwhite foods and conservation farming. J. Wildl. Mgmt., 6(2):97–109.

———. 1949. Bobwhites on the rise. N.Y.:Charles Scribner's Sons. 150pp.

———. 1954. Lespedezas for quail. U.S.D.A., Leaflet No. 373. 8pp.

——— AND KARL E. GRAETZ. 1957. Managing habitat for white-tailed deer and wild turkeys. Trans. N. Amer. Wildl. Conf., 22:412–424.

KELSEY, HARLAN P. AND WILLIAM DAYTON. 1942. Standardized plant names. Harrisburg, Pa.:J. Horace McFarland Co. 675pp.

KORSCHGEN, L. J. 1952. An analysis of the food habits of bobwhite quail in Missouri. Missouri Conservation Commission, P-R Bull. No. 7. 59pp.

LAESSLE, A. M. AND O. E. FRYE, JR. 1956. A food study of Florida bobwhite *Colinus virginianus floridanus* (Coues). J. Wildl. Mgmt., 20(2):125–131.

LAY, D. W. 1954. Quail management handbook for East Texas. Texas Game and Fish Commission, Bull. 34. 45pp.

LEE, LEVON. 1948. The fall and winter food of the bobwhite in Oklahoma. Oklahoma Game and Fish Dept. 23pp.

LEHMANN, V. W. AND HERBERT WARD. 1941. Some plants valuable to quail in southwestern Texas. J. Wildl. Mgmt., 5(2):131–135.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants. N.Y.:McGraw-Hill. 500pp.

MICHAEL, V. C. AND S. L. BECKWITH. 1955. Quail preference for seed of farm crops. J. Wildl. Mgmt., 19(2): 281–296.

MURRAY, R. W. AND O. E. FRYE. 1957. The bobwhite

quail and its management in Florida. Florida Game and Fish Commission, Game Pub. No. 2. 56pp.

NESTLER, R. B., W. W. BAILEY, A. C. MARTIN, AND H. E. MCCLURE. 1945. Value of wild feedstuffs for pen-reared bobwhite quail in winter. J. Wildl. Mgmt., 9(2):115–120.

STODDARD, H. L. 1931. The bobwhite quail. N.Y.: Charles Scribner's Sons. 559pp.

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MOURNING DOVE PRODUCTION IN A CENTRAL NEBRASKA SHELTERBELT

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This paper reports the production of the mourning dove (*Zenaidura macroura*) in a Nebraska shelterbelt for 1957 and compares it to the results found in other shelterbelts in the Plains States. Little is known of the production of this species in the North Central States (Boldt and Hendrickson, 1952).

Since nesting density varies greatly not only according to geographical sections of the country but also according to type of habitat, comparisons in this paper have been limited to work done in shelterbelts in the Plains States. Boldt and Hendrickson (*ibid.*) and Randall (1955) studied nesting doves in North Dakota shelterbelts. Dodson (1955) studied nesting doves in Oklahoma shelterbelts.

During 1956, in the vicinity of Grand Island, Nebraska, several shelterbelts produced more doves than others. A shelterbelt that seemed to have the greatest production was selected for intensive study during the 1957 nesting season. The study area was located in the Platte River Valley approximately 7 miles north of the river and 3 miles west of Grand Island. Irrigated corn, sorghums, and alfalfa were the dominant crops in the vicinity. Water was available at several abandoned sandpits and cattle-watering tanks.

The shelterbelt is 102 feet wide and 553 feet long (1.3 acres) and contains 557 trees and shrubs, plus a plum thicket. The following nine species of trees and shrubs are present in rows from north to south: a thicket of American plum (*Prunus americana*), 87 red cedars (*Juniperus virginiana*), 70 ponderosa pines (*Pinus ponderosa*), 77 green ashes (*Fraxinus pennsylvanica*), 56 black walnuts (*Juglans nigra*), 81 honey locusts (*Gleditsia triacanthos*), 47 cottonwoods (*Populus deltoides*), 72 American elms (*Ulmus americana*), and 67 Russian mulberries (*Morus alba*). Each species forms a single row except the plum thicket, two rows of cottonwoods, and one cottonwood in the row of cedars. The shelterbelt is approximately 18 years old. The estimated average size of trees and shrubs is: plum, 8 feet; cedar, 15 feet; pine, 15 feet; ash, 20 feet; walnut, 10 feet; locust, 20 feet; cottonwood, 30 feet; elm, 25 feet; and mulberry, 8 feet.

Because cattle used the shelterbelt during the winter and early spring of 1957, little ground cover was evident early in the nesting season. Livestock did not use the shelterbelt during the dove-nesting season, so that a grass and forb cover existed during the summer.

The shelterbelt was visited 30 times between April 7 and September 15 at intervals of from 3 to 9 days, depending upon nesting intensity, weather conditions, and the banding age of nestlings.

The first dove nest was noted on April 16. Throughout the season, a total of 98 nesting attempts was observed (only nests with an egg or a setting dove were recorded as nesting attempts). This represented approximately 75 nesting attempts per acre. The median nesting attempt was found on June 16. On June 6, the largest number of active nests (21) was recorded. On June 22, the largest number of new nests (10) was discovered. The last new nest was recorded on August 24. The average nest height throughout the season was 8 feet (estimated heights), and the range was from 4 feet to 16 feet.

Doves appeared to be selective as to trees preferred for nesting sites, both as to species and to individual trees. Although only 14 per cent of the trees (not including the plum thicket) were American elms, 47 per cent of the nesting occurred in this species. Ponderosa pine contained 32 per cent of the nests, yet only 13 per cent of the trees were of this species. Cottonwoods were the only species in which no nesting attempts occurred. Also, specific trees were selected as preferred nesting sites. About 24 per cent of the nest trees had more than one nesting attempt during the nesting season.

Since nest destruction (by weather or predators) and nest abandonment were difficult to differentiate, all nests not bringing nestlings to banding age were recorded as destroyed. Nestlings were banded between the age of 5 and 10 days. A total of 25 out of 98 nesting attempts (26 per cent) was successful, and 44 nestlings were banded. The production was approximately 34 doves per acre. Successful nests were considered as those in which the nestlings lived to banding size since, after being banded, they often reached the age of leaving the nest before the observer returned. The first nestling was banded on June 6; the median nestling, on July 7; and the last nestling, on September 15. Sixteen per cent of the nestlings were banded after September 1.

TABLE 1.—COMPARISON OF MOURNING DOVE NESTING AND PRODUCTION OBSERVATIONS BY SEVERAL WORKERS STUDYING DOVES IN SHELTERBELTS

Item	Randall	Boldt and Hendrickson	LaPointe	Dodson
State	North Dakota	North Dakota	Nebraska	Oklahoma
First nest	May 25	May 15	April 16	February
Nesting peak	July	Aug. 13–19	June 6	last July, early Aug.
Last nest	Sept. 5	Sept. 25	Sept. 15	few after Sept. 15
Tree preference	little evidence showing preference	Chinese elm, American elm Russian olive	American elm, ponderosa pine	Osage orange, mulberry, juniper, Chinese elm
Production per acre	28.2	1	34	1.12–1.52
Percentage successful nests	77	58	26	15
No. young per successful nest	1.5	1.8	1.8	—
Average height of nests	—	5 feet	8 feet	—

The percentage of nesting success by months was calculated to be: April, 0 per cent; May, 38 per cent; June, 15 per cent; July, 20 per cent; and August, 42 per cent. This conflicts with observations of other workers (Anon., 1957:30), who have noted that nesting success becomes higher as the season progresses. No nests were started in other months. Estimates of the production by months (hatching dates) were: May, 4; June, 17; July, 11; August, 10; and September, 2.

Observations of dove nesting and production in shelterbelts were compared to those of several other workers (Table 1). It was concluded that nesting success and production even in similar habitat, such as that provided by shelterbelts, are extremely variable.

SUMMARY

A shelterbelt near Grand Island, Nebraska, was selected for intensive study during the 1957 mourning dove nesting season. The study area was visited 30 times between April 7 and September 15. The median attempt was observed on June 16. Doves preferred American elms and ponderosa pine as nesting sites. A total of 25 out of 98 nesting attempts (26 per cent) was successful, and 44 nestlings were banded. The production was approximately 34 doves per acre.

LITERATURE CITED

ANONYMOUS. 1957. Mourning dove investigations 1948–1956. S.E. Assoc. Game and Fish Comm., Tech. Bull. 1. 166pp.

BOLDT, WILBUR AND GEORGE O. HENDRICKSON. 1952. Mourning dove production in North Dakota shelterbelts, 1950. J. Wildl. Mgmt., 16(2):187–191.

DODSON, MONTE M. 1955. Oklahoma migratory game bird study. Report for 1949–1953 under P-R W-32-R. Oklahoma Game and Fish Dept. 51pp.

RANDALL, ROBERT N. 1955. Mourning dove production in south central North Dakota. J. Wildl. Mgmt., 19 (1):157–159.

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A PORTABLE APPARATUS FOR PHOTOGRAPHING VEGETATIVE QUADRATS

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In an effort to supplement the field record of plant species location in vegetative quadrats, an apparatus was developed for obtaining vertical photographs of the plots, giving a permanent record of plant species location and density. This apparatus consists of three parts: the camera support, telescoping poles, and base plates.

The camera support is constructed of a treated 1-inch × 2-inch board, 68 inches long, to which is attached an aluminum box that houses the camera, and two ¾-inch metal sleeves, 2 inches in length. The aluminum camera-housing box is made of 0.051 SO alloy. A small hole is provided at the rear of this box for the tripod screw, in order that the camera may be held firmly in place. An opening on the side is provided for focusing.

The telescoping metal poles consist of two sections of ½-inch electrical tubing, 7 feet in length, and two pieces of ¾-inch tubing, 57 inches in length. These latter two sections are provided with three ¼-inch × 28 × ½-inch wing bolts, spaced 15 inches apart, which secure the ½-inch tubing in place when it is telescoped to the desired height.

Two metal base plates or "feet," made from ⅛-inch boiler-plate steel, serve to hold the apparatus in place once it is set up. These base plates are

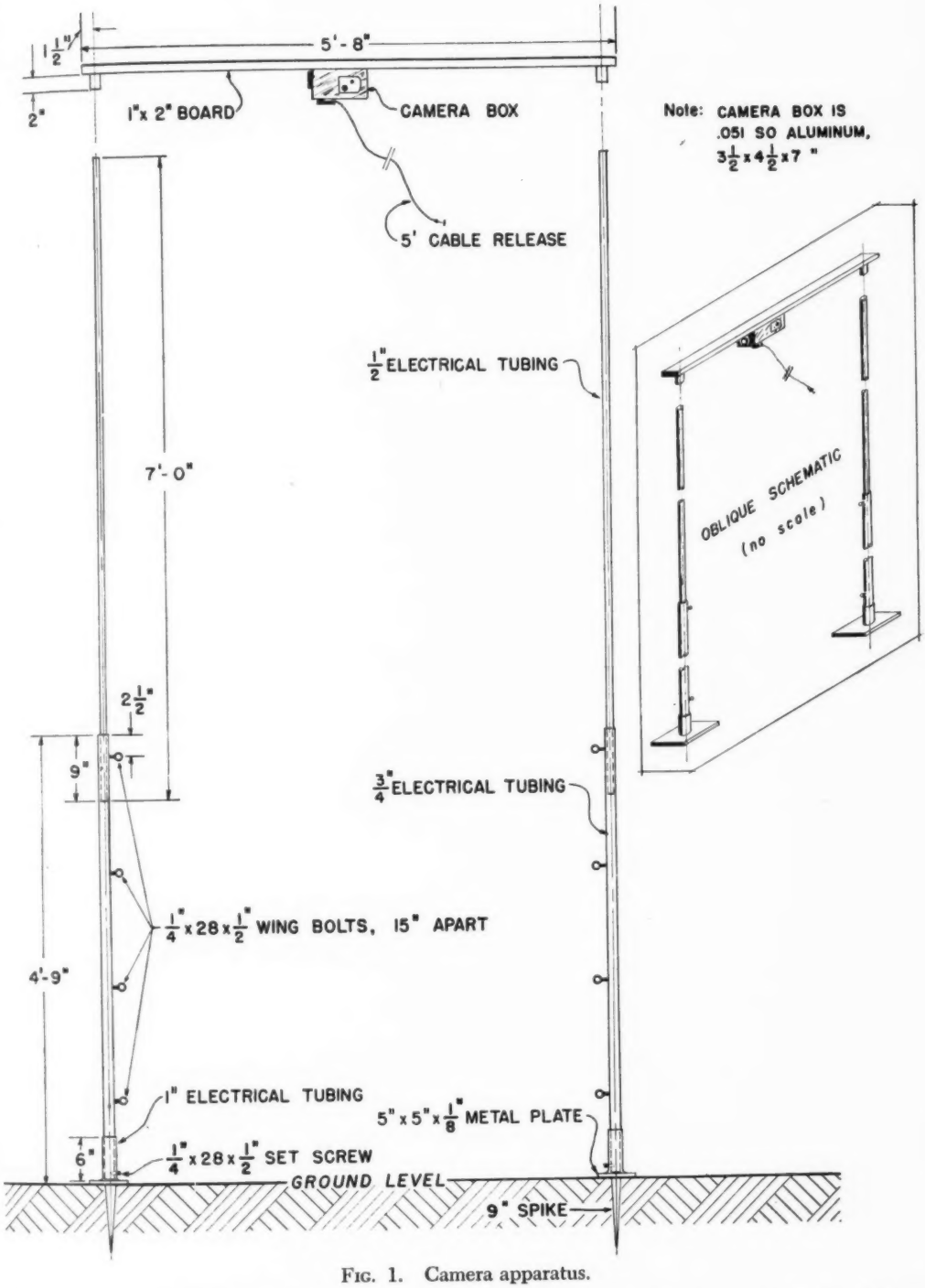

FIG. 1. Camera apparatus.

5 inches square and are fitted in the center with a 1-inch metal sleeve, 6 inches long, into which the bottom ends of the telescoping poles are inserted. It was found necessary, in the soft peat soils of the Everglades, to attach a ½-inch metal spike, 9 inches long, to the bottom center of each

"foot" in order that the apparatus might be secured in a firm position.

This apparatus is most applicable when quadrat size does not appreciably exceed one square meter. It can be constructed, however, to photograph larger plots by increasing the length of the telescoping poles controlling the height to which the camera can be raised over the plot. In such cases the camera can be prefocused for specified distances and for coverage prior to placing it in the holding box. The telescoping poles can then be raised to the designated height, and the camera shutter tripped with a cable release or an electronic device.

Dimensions for the camera holding box, given in Fig. 1, are for a twin lens, 120 Graflex, but can be modified to fit almost any type of small camera. In our Everglades studies, only color slides were taken as we found that black and white did not give satisfactory contrast.

Vertical photographs of vegetation quadrats are most applicable where low-growing herbaceous plants are involved. When the height of plants exceeds 3 feet, it is difficult to obtain satisfactory depth of field.

This camera apparatus is easily handled in the field and is inexpensive to construct.

The assistance of Richard Eichhorn, Florida Game and Fresh Water Fish Commission and W. H. Speir, Agricultural Research Service, is acknowledged.

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TOOTH IMPRESSIONS AS AN AID IN THE DETERMINATION OF AGE IN DEER[1]

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The development of a method for determining the age of deer by tooth wear and replacement (Severinghaus, 1949) has made it possible to determine growth rates, breeding dates, population-age composition, productivity, and other facts from deer shot by hunters. Often this information cannot be acquired because of a lack of sufficiently trained personnel. Such a situation exists in Maryland, where deer hunting is spread throughout the state and a large number of trained technicians are required for only a day or two in order to gain an adequate sample of the deer harvest. Untrained men are available to gather and record data and, if some method of recording tooth characteristics were available, a trained biologist could determine the age of the deer from the data sent in to the laboratory. Collecting the lower jaws was impractical because hunters objected to mutilation of their deer. Wax or clay impressions of teeth seemed to be a possible solution, and therefore experimentation was undertaken with various materials. A method was gradually developed and improved whereby impressions could be made of the teeth of deer in the field. The impressions were sent to the laboratory where a biologist determined the age of the deer from plaster casts of these impressions. This method has proved so successful that it has been used for 3 years, and approximately 1,000 impressions have been made so far.

Among the various impression materials that were tried, the most satisfactory proved to be the modeling clay sold in toy departments. Most of the brands tested were satisfactory, but since a few were not, the author suggests that anyone intending to try this technique should first experiment with the various brands available before going into the field. The requirements of suitable modeling clay are that it should be fine-grained, smoothly plastic, and it should not be lumpy, sticky, or miscible with saliva or blood.

The modeling clay was pressed into sheet metal, U-shaped channels about 5 inches long, ½ inch

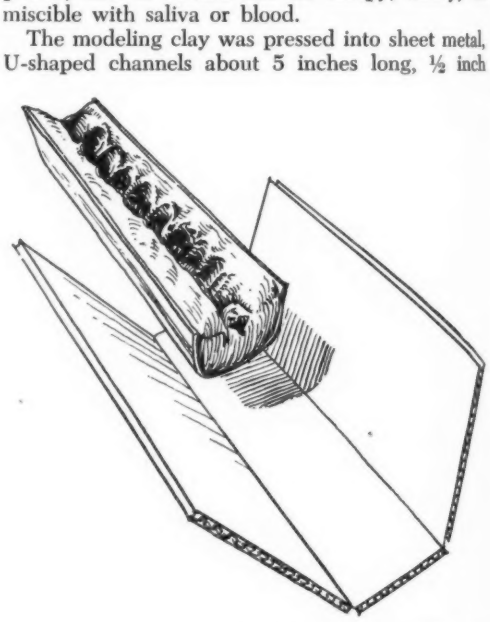

FIG. 1. U-shaped metal channel containing modeling clay with the impression of the molars and premolars of the lower jaw of a deer. The method of scoring and folding the cardboard around the channel is shown.

[1] Acknowledgment is due Harold J. Elser, whose suggestions were most helpful in development of this technique. Contribution No. 114, Department of Research and Education.

deep and ¾ inch wide. The channels can be made either from sheet aluminum (0.019 inch thick), which can be cut with household scissors, or from galvanized sheet iron (27 gauge). While the deer's mouth was held open by means of a jaw wrench of the type designed by Severinghaus, a metal channel filled with modeling clay was pressed firmly down over the molars and premolars of either side of the lower jaw. The channel was then carefully lifted, revealing a mold of the teeth (Fig. 1).

Impressions can also be made of the incisors and, for this, a longer channel, 7 inches long, should be used so that the impressions of the back teeth and front teeth will be in the same channel. Data such as date, locality, sex, and weight can be recorded directly on the outside of the metal channel with a glass marking pencil.

Since deer hunting usually takes place in cold weather, the modeling clay often becomes too hard for making suitable impressions. To keep the plasticene at the desired consistency, warming boxes were used. These were insulated boxes with wire shelves to permit circulation of warmed air and a hinged door for removal of the clay-filled channels. The boxes were heated with two or three light bulbs wired in parallel so that one or two bulbs could be unscrewed, thus permitting adjustment of the temperature. Overheating caused the modeling clay to become too soft and prevented formation of suitable impressions. The boxes were connected to electric outlets by means of extension cords. Where electricity was not available, alcohol lamps and sometimes stoves or radiators were used.

After the impressions were made, the channels were cooled immediately and stored in a box to prevent obliteration of the details by rough handling. The clay impressions retain their form indefinitely.

Plaster casts were made from the impressions as follows: Pieces of corrugated cardboard were cut to the same length as the sheet metal channels and 5 inches wide. The cardboard was scored with a pen knife, making 2 parallel cuts ¾ inch apart across the middle of the cardboard. The cardboard was then bent around both sides and the bottom of the channel, forming a wall along the sides of the mold. Plasticene dams were made to close the open ends of the cardboard form. A stout rubber band held the cardboard form together (Fig. 2). Plaster of Paris was then mixed with water and poured into the mold.

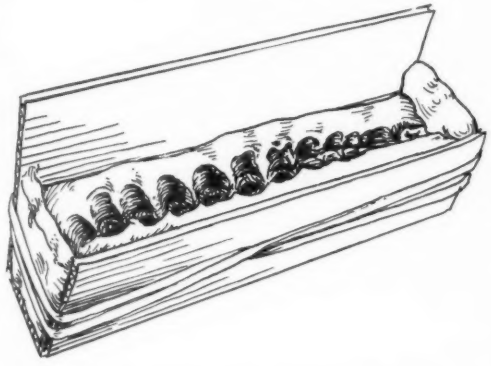

FIG. 2. The impression with modeling clay dams at each end of the cardboard ready for the plaster of Paris to be poured.

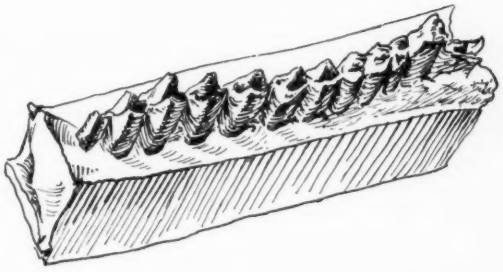

FIG. 3. A plaster cast of the lower teeth of a deer.

After two or three hours, the plaster of Paris has set and the cast can be removed (Fig. 3). The result should be a replica of the deer's teeth. If the plaster has not been properly prepared, air bubbles may prevent the plaster from filling the deep recesses of the impression but this is usually not important. Light tapping of the mold before the plaster has set will loosen some of the bubbles so that they can float to the surface. Data can be written with a pencil directly on the plaster cast.

The ages of deer are determined from the casts. However, because the casts have no color to show dentine and enamel, some confusion may be experienced at the very beginning, but this can soon be overcome by careful comparison of the casts with actual jaws. The casts can be saved, if desired, for future reference. The greatest advantage of this technique is that unskilled help can be used to gather data in the field, while the ages of the deer may be determined with precision by one trained biologist.

SUMMARY

A method was developed for making impressions of the lower teeth of deer. Plaster casts of these impressions are replicas of the deer teeth. This method makes possible the use, in widely scattered localities, of untrained personnel, who can collect data and send it to a central office where one man determines the age of all the deer.

LITERATURE CITED

SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Mgmt., 13:195–216.

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SOME WEIGHTS AND MEASUREMENTS OF DESERT BIGHORN SHEEP (*OVIS CANADENSIS NELSONI*)

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The weights and measurements in Tables 1 and 2 are presented with the hope that they may prove useful for comparisons between different herds of the same species and should be indicative of the relative value of different ranges and habitat for desert bighorns. They will also be useful to taxonomists in establishing more concrete differences between the races of bighorn sheep. The literature at present refers to one race as slightly larger or slightly smaller than another race. In some instances only approximate weights are given. With the accumulation of quantitative data on the subject, average differences should result.

Ages are not given as there is some doubt as to the validity of field aging techniques for bighorn sheep. All weights and measurements are of

TABLE 1.—WEIGHTS AND MEASUREMENTS OF RAMS, 1956 (expressed in pounds and inches)

Date	Live Weight	Dressed Weight	Girth	Height at Front Shoulder	Hind Foot	Tail Length	Total Length
			HUNTED				
Dec. 11	155	112	38½	35¾	13¾	3	54
Dec. 3		108	40	37½	14½	3½	57½
Dec. 6	155	102	40½	38½	15	3¼	59½
Dec. 6	146	100	40	35	14½	3½	57
Dec. 15	150	102	38¼	38	15¼	3¼	57
Dec. 12		106	38	35¼	13½	2¾	52
Dec. 13	153	108	37	36	14½	3	56
Dec. 8	134	86	39½	37½	15½	3	55½
Dec. 13		110	40	37½	16	4½	58
Dec. 15	168	114	41¼	38¼	15¾	3	60
Dec. 19	162	113	40	34½	14¼	3	56
Dec. 3	148	95	41	33¼	14	3	54
Dec. 1	172	114	38¾	38¼	15½	3¾	61
Dec. 2		124					
Dec. 2		118					
Dec. 1		108	40	36	14	3	53
Dec. 1		112	41	37	13½	3	57
Dec. 12	168	110	41	35¾	15	3	57
Dec. 3	127	85	38	31	14½	3	56
Dec. 2	148	92	39¼	35	15½	3½	62¼
Dec. 1		100	41	36½	14	3	53½
Dec. 1		98	38	35½	14¾	2¾	55½
Dec. 11		95	37½	36	14½	4	61
Dec. 6		86	37	36½	14½	2½	58¼
Dec. 7	166	118	41	39	15½	3½	63½
			TRAPPED				
June 14	143		39¾	38	15⅛		
July 9	146		39½	36	13⅞		
July 10	190		41¼	38	15¼		
July 10	181		41½	37½	15½		
July 10	140		39	33½	13½		
July 10	179		41⅛	37¼	15		
July 12	168		41½	37½	15		
July 12	152		40	35½	14¾		
July 12	141		38	36¼	14½		
July 17	158						
July 18	162						
July 19	144		40	34¼	12½		
Maximum	190	124	41½	39	16	4½	63½
Minimum	127	85	37	31	12½	2½	52
Average	156	104.6	39½	36¼	14⅝	3¼	57⅛

sexually mature animals. These figures were obtained from bighorns trapped or shot during 1956. All animals are from the Sheep Range in the Desert Game Range, a U.S. Fish and Wildlife Service refuge, located north and west of Las Vegas in Clark and Lincoln Counties, Nevada.

These sheep range from about 5,000 feet to nearly 10,000 feet. Food throughout the range is considered very adequate quantitatively even in dry years. However much may be lacking qualitatively. Average annual precipitation in this area is 4.23 inches. In 1956 the total precipitation was 0.17 inch. There are usually two growing seasons, one in early spring and one following the summer rains. Lambs are dropped from February to July, and rutting takes place from late July until early December.

The "hunted" rams in Table 1 were taken during the special hunt December 1–22, 1956. The remainder of the sheep in Table 1 and the sheep in Table 2 were trapped.

Measurements on trapped animals were held to a minimum to prevent shock resulting from excessive handling. The additional measurements on the rams in Table 1 were taken in the field at the time the sheep were shot. Dressed weights are "hog dressed."

A captive 9-year-old ram at the Corn Creek Field Station weighed 176 pounds. This ram, which was captured as a lamb, always had water and natural food, plus supplemental alfalfa and rolled oats.

The average weight of trapped rams was 5 pounds more than rams taken during the controlled hunt. Trapped rams were weighed during summer, hunted rams in December following the rutting season.

TABLE 2.—WEIGHTS AND MEASUREMENTS OF TRAPPED EWES, SUMMER 1956 (expressed in pounds and inches)

Date	Live Wt.	Girth	Height[1]	Hind Foot	Dry or Lactating
June 6	109	35½	34	13¼	D
June 6	86	34	33	13½	D
June 12	99	36½	34	14⅛	L
June 15	74	33½	34	13¾	L
July 5	100	37¼	32	13⅛	D
July 6	76	34	33½	13½	D
July 17	102				D
July 17	96				D
July 17	100				D
July 19	113	38	33½	13	D
July 19	88	35½	32	12½	D
Sept. 7	100	35	34	14½	D
Nov. 7	114	36¼	33½	13¾	D
Nov. 7	98	34½	33	13½	D
Nov. 9	94	40	34	14	D
Maximum	114	40	34	14½	
Minimum	74	33½	32	12½	
Average	96.5	35¾	33⅜	13½	

[1] At front shoulder.

The dressed weight of 14 Nelson bighorn rams was 68 per cent of the live weight. We conclude that, as a rule of thumb, rams dress out at 2/3 of their live weight.

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A MARKING TECHNIQUE FOR BIGHORN SHEEP

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On the Desert Game Range in southern Nevada, administered by the U.S. Fish and Wildlife Service, we have been conducting field studies on the Nelson bighorn sheep (*Ovis canadensis nelsoni*). Early in the study we sought a marking technique that would provide a sound basis for gathering observational field data. A marking system was needed that would meet the following requirements: mark each animal as a distinct individual, last the life of the animal, and be readily and easily seen in the field.

The fact that sheep do not shed their horns suggested the possibility of a horn brand similar to that used on cattle. An old sheep skull with the horns attached was experimentally branded. It was easily read some 500 yards away with a 30× spotting scope. A different brand number for each sheep solved the first two requirements. The next step was to devise something that would catch the eye, making a branded animal stand out in a group of sheep. For this we tried brightly colored plastic ear streamers similar to those Craighead and Stockstadt (1956) had used to mark geese successfully in Montana. In addition, a stock-type ear tag was placed in the right ear of the animal for further identification.

When the sheep are trapped, they are quickly tied and blindfolded. The blindfold quiets the animal and makes drugging unnecessary. The branding irons are heated in a fire or with a weed burner. It is very important to heat the iron until it is copper red, as an underheated iron does not make a good brand, while a good hot iron burns a clean legible brand without any apparent pain to the animal.

The first bighorn trapped was branded No. 1, and each successive one was branded with its individual number. Number brands were burned on the outside of each horn. Ewes were branded

FIG. 1. Ewe showing brand and stock-type ear tag in right ear.

with a 7/8-inch iron and rams with a 2-inch iron. The plastic streamer was inserted in a small slit in the left ear and secured with a jess knot (Craighead and Stockstadt, *ibid.*). The stock-type tag was clamped in the right ear of the animal.

Sheep numbered 1 to 5 were not marked with the plastic streamer and have consequently been more difficult to locate. They have been seen and identified again only because groups of sheep were thoroughly scanned with a 30× spotting scope. On the other hand, 25 animals with the plastic streamer have been spotted at a great distance, both with the naked eye and with field glasses. They were then carefully stalked until the brand could be read. Several observations of marked animals have also been made when the sheep took flight. Although it was impossible to read the brand, the streamer provided a record of movement from the trap site, as a different colored plastic streamer was used at each trap.

The only change we contemplate in the above will be to outline the brand with paint so that the number can be more easily read.

Some of the 25 sheep have been ear-tagged for over a year, and to date only one streamer has pulled loose. This one was put on by an inexperienced helper, and the ear slit was not properly made.

We wish to thank Warren E. Kelly, Nevada Fish and Game Commission, for his help in experimenting with brands.

LITERATURE CITED

CRAIGHEAD, JOHN J. AND DWIGHT S. STOCKSTADT. 1956. A colored neckband for marking birds. J. Wildl. Mgmt., 20:331–332.

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ULCERATIVE ENTERITIS IN THE PHEASANT, BLUE GROUSE AND CALIFORNIA QUAIL

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Ulcerative enteritis is considered a very formidable disease of quail in captivity, but insofar as we can ascertain it has not been reported for the pheasant (*Phasianus colchicus*), blue grouse (*Dendragapus obscurus*) nor wild populations of California quail (*Lophortyx californicus*). The early report on ulcerative enteritis by Morse (1907) pertains to birds held or reared artificially in captivity. He states that "postmortem examination has up to the present time demonstrated the presence of quail disease in the common bobwhite (*Colinus virginianus*), the California quail (*Lophortyx californicus vallicola*), the Gambel quail (*Lophortyx gambeli*), the mountain quail (*Oreortyx pictus*), the scaled quail . . . (*Callipepla squamata*), and the sharp-tailed grouse (*Pedioecetes phasianellus campestris*)." The following additional reports on this disease also refer to birds in captivity: Mexican quail (Shillinger and Morley, 1934), ruffed grouse (Levine, 1932; LeDune, 1933), and turkey (Shillinger and Morley, *op. cit.*). Rosen and Bischoff (1949) conducted post-mortem examinations of two California quail from a game farm in California and attributed death to ulcerative enteritis. Bump, Darrow, Edminster, and Crissey (1947), who claim that ulcerative enteritis attacks the chukar partridge, state that outbreaks in quail and grouse ". . . have occurred only in artificially propagated birds although Green and Shillinger (1933) in Minnesota have reported finding ulcerative enteritis in a wild [ruffed] grouse."

Morley and Wetmore (1936) designated *Corynebacterium perdicum* as the organism responsible for

[1] Acknowledgment is made to C. W. McNeil, Zoology Department, State College of Washington, for his help in studying the parasites of the blue grouse.

ulcerative enteritis, but the subsequent investigations of Bass (1939) and Durant and Doll (1941) did not substantiate this. The latter studied the gross pathology, bacteriology, and histopathology of ulcerative enteritis and concluded that the agent was probably bacterial in nature, although they were unable to isolate the organism. Bass (1941) reported a gram-negative, anaerobic bacillus occurring with the disease as a possible etiological agent. At present the etiology of this disease remains unknown.

In August 1949, one of us investivated a mortality problem occurring in a flock of 12,050 young pheasants that were being held on a 10.9-acre rearing range at the New York State Delmar Game Farm, Delmar, New York. These birds were put on the range when they were approximately 4 weeks of age on July 29, 1949. On August 14 an unusual mortality became evident and continued until August 23 when the birds were treated with sulfaquinoxaline sodium at the rate of 1 fluid ounce per gallon of water and the survivors were moved to a 15-acre field on which no birds had been reared that year. The mortality decreased, and the birds were all shipped for liberation by September 13, 1949.

The examination of eight specimens that were found sick and dying showed the typical lesions of ulcerative enteritis. They were all in good flesh, well feathered, and their average weight was 385 gms. In one bird, the pathology included many discrete necrotic ulcers, some of which showed hemorrhagic areas that were generally confined to the lower third of the intestine. In the others, the necrotic ulcers were found in the duodenum, ileum, rectum, and caeca, the lining of which was thickened. In another bird, an ulcer had formed an occlusion of the intestine with a distension and swelling above the stoppage. No helminths were recovered, and only a few coccidia, probably *Eimeria* sp., were found. Fig. 1 shows the typical lesions of ulcerative enteritis found in pheasants.

During the fall of 1957, post-mortem examination of 10 blue grouse revealed pathology characteristic of acute ulcerative enteritis. These grouse, two adult females, four juvenile females, and four juvenile males, were trapped between July 18 and August 3, 1957, on breeding range in the Methow Valley east of Winthrop, Okanogan County, Washington. They were placed temporarily in a covered pen 10 feet × 10 feet in size and fed on wheat, fruits of native shrubs, and freshly cut clover. On August 5, 1957, they were transported by automobile to Pullman in southeastern Washington where they were placed in a covered pen 15 feet × 60 feet in size. The pen, which was newly constructed and had not been used by any other animals, contained a sparse stand of annual weeds, some alfalfa, and a little grass. Water, grit, wheat, peas, and fruits of snowberry (*Symphoricarpos* sp.) and hawthorn (*Crataegus* sp.) were placed in the pen.

FIG. 1. Lesion of ulcerative enteritis in intestine of pheasant.

The grouse appeared to grow well, developed good plumage, and seemed alert and active. However, on September 26, 1957, a juvenile male was found dead in the pen and a juvenile female was obviously in critical condition. She was sluggish and, when approached, did not fly but ran feebly for about 15 feet and then fell upon the ground. Both birds were removed from the pen and examined immediately. The small intestine, particularly the jejunum and upper ileum, of each specimen was acutely involved. Old and recent lesions were present; in the male practically all of the intestinal mucosa was sloughed away in the upper ileum which was very thin, contained a few small yellowish or whitish areas which had a nodular appearance, and showed a few hemorrhagic areas up to eight mm. in diameter. Attempts to find trichomonads or coccidia or to isolate pathogenic enteric bacteria from the infected areas were unsuccessful. The intestines of the female had an infestation of two cestodes and a nematode, which were identified by Allen McIntosh of the Agricultural Research Center, Beltsville, Maryland, as *Rhabdometra nullicollis, Raillietina* sp., and *Heterakis gallinarum*, respectively. Six individuals of *R. nullicollis* were found in the intestines of the male. The parasites were probably not related to the pathology that occurred in these grouse. Averaged differential white blood counts of the female and those from a healthy male blue grouse collected

TABLE 1.—COMPARISON OF DUPLICATE DIFFERENTIAL WHITE BLOOD COUNTS OF THE NORMAL AND DISEASED BLUE GROUSE

Leucocyte	Percentage in	
	Infected Female	Healthy Male
Neutrophils	32	54
Lymphocytes	55	35
Monocytes	12	5
Eosinophils	1	4
Basophils	—	2

and examined on October 19, 1957, are shown in Table 1. These differential white blood counts are presented for consideration and not as definitive counts representative of the normal and diseased blue grouse. Although there was no subcutaneous or visceral fat present, neither bird appeared emaciated, and no other abnormalities were found.

By October 7, 1957, all 10 of the grouse had died. Post-mortem examinations showed that these grouse had evidently died from intestinal infection, which appeared almost precisely the same in each case. Attempts to save the last eight grouse by administration of streptomycin, the therapy recommended by Kirkpatrick, Moses, and Baldini (1952) for ulcerative enteritis in bobwhite quail under captive conditions, failed.

During the winter of 1957–58, typical pathology of ulcerative enteritis was encountered in a population of wild California quail in southeastern Washington. The population of approximately 150 quail comprised a single flock that lived in a canyon 2 miles upstream from the mouth of George Creek, Asotin County. Range and wheat land dominate the region, and cottonwood (*Populus* sp.), alder (*Alnus* sp.), and other shrubs, in addition to weeds and grass, provide winter cover for quail and other gallinaceous birds along the bottom of the canyon.

A flock of 3,000 domestic turkeys, living under crowded conditions in the canyon, had acquired fowl cholera with a resultant loss of over 1,000 birds. Since the turkeys were confined in an enclosure adjacent to George Creek on the quail's winter range and both fed daily from the turkey feeders, an investigation was conducted to determine the possible occurrence of cholera in the quail. On December 13, six quail were collected, and 14 dead quail were found at the edge of the enclosure under dense thickets of shrubs and vines. Five of the dead quail were partly eaten by scavengers and not usable for diagnostic purposes. The other nine were entire, but they showed no evidence of fowl cholera at necropsy, and only negative results were obtained in extensive bacteriological tests. However, intestinal lesions, characterized by extensively eroded and ulcerated areas, were observed in all of these nine birds and one of the six quail collected by shooting.

Nineteen additional dead quail were found under thickets at the edge of the turkey enclosure on December 27, and a careful census of the canyon with the aid of a trained dog produced a single covey of 35 to 40 quail. By January 18, 1958, mortality in the quail had evidently ceased, for the covey had not declined in numbers and no dead birds were found.

Kirkpatrick, Moses, and Baldini (1950) report that ulcerative enteritis seems particularly virulent among flocks of young quail in captivity during late summer and especially when the birds are overcrowded. Their experiences indicate that after mortality begins, it continues for several weeks until a majority of the original flock is dead. The remaining birds, either those that have recovered and established some immunity, or that were not susceptible, thrive and continue their development. According to their tests, such birds apparently are immune to subsequent experimental exposure.

Since there was an observed mortality of about 73 per cent in the population of quail at George Creek, and since 29 of the 33 quail found dead were juveniles, it is evident that their response in the wild to ulcerative enteritis was strikingly similar to the response of pen-reared bobwhite quail to this disease, as described by Kirkpatrick, Moses, and Baldini (*ibid.*).

The concentration of quail at George Creek and the frequent reference to crowding of birds on game farms in published reports of ulcerative enteritis indicate the importance of density to ulcerative enteritis and suggest that the coaction of these two factors could be highly significant in the control of certain wild populations of gallinaceous birds. W. A. Halsey, a rancher in George Creek Canyon who owns the land on which this study was conducted, told us that he had observed many large concentrations of California quail along George Creek during previous winters and that they had frequently disappeared or dwindled to small coveys by spring. Shillinger (in discussion following report by Shillinger and Morley, *op. cit.*) states that, "The most prominent features of the disease that we have encountered have been the violent outbreaks on game farms and in flocks of birds that were shipped in concentrated numbers for restocking purposes."

LITERATURE CITED

BASS, CHARLES C. 1939. Observations on the specific cause and the nature of "quail disease" or ulcerative enteritis in quail. Proc. Soc. Exp. Biol. and Med., 42(2):377–380.

———. 1941. Specific cause and nature of ulcerative enteritis in quail. Proc. Soc. Exp. Biol. and Med., 46:250–252.

BUMP, GARDINER, ROBERT W. DARROW, FRANK C. EDMINSTER, AND WALTER F. CRISSEY. 1947. The ruffed grouse. New York State Cons. Dept. 915pp.

DURANT, A. J. AND E. R. DOLL. 1941. Ulcerative enteritis in quail. Univ. Missouri Agric. Exp. Sta., Res. Bull. No. 325. 27pp.

GREEN, R. G. AND J. E. SHILLINGER. 1933. Minnesota wild-life disease investigation [monthly report], October, 1933. U.S. Dept. Agric., Bur. Biol. Surv., Washington, D.C. 9pp. (mimeo.)

KIRKPATRICK, C. M., H. E. MOSES, AND J. T. BALDINI. 1950. Streptomycin studies in ulcerative enteritis in bobwhite quail. I. Results of oral administration of the drug to manually exposed birds in the fall. Poultry Sci., 29(4):561–569.

———. 1952. Streptomycin studies in ulcerative enteritis in bobwhite quail. II. Concentrations of streptomycin in drinking water suppressing the experimental disease. Amer. J. Vet. Res., 13(46):102–104.

LEDUNE, E. K. 1933. Ulcerative enteritis in ruffed grouse. Vet. Med., 30(9):394–395.

LEVINE, P. P. 1932. A report on an epidemic disease in ruffed grouse. Trans. Amer. Game Conf., 19:437–441.

MORLEY, L. C. AND P. W. WETMORE. 1936. Discovery of the organism of ulcerative enteritis. Proc. N. Amer. Wildl. Conf., pp. 471–473.

MORSE, G. B. 1907. Quail disease in the United States. U.S. Dept. of Agric., Bur. Anim. Ind., Cir. No. 109. 11pp.

ROSEN, MERTON N. AND ARTHUR I. BISCHOFF. 1949. Field trials of sulfamethazine and sulfaquinoxaline in the treatment of quail ulcerative enteritis. Cornell Vet., 39(2):195–197.

SHILLINGER, J. E. AND L. C. MORLEY. 1934. Studies on ulcerative enteritis in quail. J. Amer. Vet. Med. Assoc., 37(1):26–33.

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FERTILE ANTLERED MULE DEER DOE

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An antlered mule deer (*Odocoileus hemionus*), followed by two fawns and believed to be a doe, was first observed December 11, 1951, on Jump Up Divide, North Kaibab Forest, Arizona, during a posthunt deer survey conducted by the Arizona Game and Fish Commission. In the same area on December 2, 1952, during the annual posthunt deer survey, an antlered deer followed by two fawns was again observed and thought to be a doe. The antler development was identical with that of the deer seen in 1951, and it was assumed that the two observations were of the same animal. During 1952 and 1953, in the same area, several additional observations of an antlered deer that appeared to be a doe were reported to the writer.

On March 2, 1953, an antlered doe was captured in a deer trap located on Jump Up Divide. The general antler conformation was the same as that of the deer seen during the previous observations. Her external reproductive organs were normal female structures. Following her capture, the doe was ear-tagged and released for deer-migration-study purposes.

On November 15, 1953, during the North Kaibab deer hunt, this tagged antlered doe was shot in Hole-In-The-Rock Canyon, 15 miles from the site of release. Unfortunately, the reproductive organs were not recovered for determination of the doe's rate of ovulation and degree of breeding success. It was, however, evident that the doe had fawns during 1953 in that her udder was still slightly enlarged and contained milk. The dentition of the doe indicated that she was 5–6 years of age.

The length of the left antler measured 0.5 inches, while the length of the right antler measured 2.3 inches. The base of the right antler was malformed with several horizontal projections from the main antler, the longest of which measured 0.9 inches. Both antlers were covered by velvet. The right antler was injured when the doe was trapped and tagged. Examination of the antler at the time of the injury showed the velvet antler covering to be living tissue with an extensive circulatory system. The antler core was hard and appeared to be fully developed. Eight months later the injured velvet hung down from the tip in dry hard flaps, leaving a hard, well-formed antler tip exposed. The uninjured velvet was still healthy living tissue. This appeared to indicate that a cyclical antler growth and shedding did not occur.

Records of antlered doe deer indicate that they may bear young. Those animals having antlers that remain in the velvet usually are sexually mature females, while those having polished antlers are apparently hermaphroditic or pseudohermaphroditic (Wislocki, 1954, 1956). In mule deer, doe antler development may vary from the nubbin-type antler of the doe reported in this note to large well-formed antlers reported by Swank (1958).

The external physical characteristics of this antlered doe correspond to the descriptions given by Wislocki for fertile antlered does. In addition, the fertility of this antlered doe persisted during three breeding seasons with no apparent shedding of antlers or velvet.

LITERATURE CITED

SWANK, WENDELL G. 1958. The mule deer in Arizona chaparral. Arizona Game and Fish Comm., Wildlife Bull. No. 3. 109pp.

WISLOCKI, G. B. 1954. Antlers in female deer. J. Mammal., 35:487–495.

———. 1956. Further notes on antlers in female deer of the genus *Odocoileus*. J. Mammal., 37:231–235.

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BOOK REVIEWS

The Mule Deer in Arizona Chaparral. By Wendell G. Swank. State of Arizona Game and Fish Department, Phoenix, Wildlife Bulletin No. 3. 1958. 109pp.

Here is a highly informative bulletin based on five-years' research on mule deer in Arizona. Findings have been skillfully blended with those from other states to make for interesting reading for both the technician and layman. Playing no small part in the bulletin's appeal are the many excellent black and white sketches by Larry Toschik, together with a number of good photographs and attractive graphs.

The reader is first taken through a descriptive background of the chaparral or brushland areas of Arizona, and of the specific study areas. This is followed by a very good general discussion of herd-mortality factors and by detailed accounts of population dynamics for the several herds under study. The studies pointedly demonstrate that herds of the state are generally being underharvested, and the author presents many forceful arguments for stepping up hunter take.

Deer workers elsewhere will likely be surprised at the extremes found in annual herd mortality and productivity—conditions created in part by fully or overstocked ranges, but largely due to periodic droughts.

This reviewer's criticisms are minor in nature and chiefly concern some of the computations. For example, yearling female percentages in Tables IX and XI for the North Kaibab herd should have been identical for each of the five corresponding years, and in Tables XVI and XIX for the Bill Williams herd; yet there was agreement in but one of the 10 sets of values. Early fawn mortality on the Kaibab was computed at 46 per cent for 1953 on the basis of a fetal study and fawn survival by late summer. The computable loss was actually 26 per cent because immature, nonproductive does had been excluded from the fetal-rate sample but included in the late-summer field counts of does and fawns.

In still another instance, the "4" in "45.7" (Table X, yearling does per 100 adult does) was inadvertently omitted leading to a computed over-winter fawn loss of 86.3 per cent, when actually there was no computable mortality because field records gave a lower proportion of fawns entering winter than of yearlings the following fall.

The two graphs in Fig. 30 have been negligently reversed, as have the values in Fig. 37 for the Mingus Mountain herd. Few misspellings or grammatical and typographical errors were noted. However, Dr. Cottam might raise an eyebrow to see his name spelled "Cottom" and "corpora lutea" was used in one instance when the singular was intended.

Ovarian analyses revealed corpora luteal scar counts of 2.5 to 3.0 per mature doe for several samples. Rates in excess of 2.25 are clearly out of line (for samples of 10 or more does) with known corpora lutea counts made elsewhere during pregnancy. Higher rates obtained from does in Arizona a few months after parturition strongly suggest the inclusion of some scars older than those from the breeding season just past. It is quite evident in mule deer that regression of the corpora lutea is not complete in many instances for as long as two years and perhaps even longer. Successful application of Cheatum's technique to mule deer will hinge on one's ability to segregate current scars from those of older generations.

Some might take issue with the author's use of prehunt rather than posthunt deer-population values as is commonly done in western states. Not only are direct comparisons of research findings made more difficult through use of different population bases, but posthunt values seem to reflect average yearlong numbers more realistically than prehunt values. Prehunt values are the maximum and commonly exist for only 4 months. Deer–livestock competition is a hot issue on many western ranges, and more equitable comparisons of livestock and big game numbers would be afforded if fawns were not counted until about 6 months of age (or after the hunt), as practiced with livestock permitted on public ranges.

Dr. Swank defines "productivity" as the ratio of the number of animals reaching adulthood (yearling age) to the mature animals of the herd, expressed as a percentage. This definition is similar to one adopted by the Society's Committee for Technical Nomenclature for "net production" (J. Wildl. Mgmt., 21:375) which reads: "The number of individuals . . . that reaches maturity and is thus available for harvest." Net productivity based upon yearlings rather than fawns, as many authors calculate, is commendable, for the influence of juvenile mortality is eliminated. Even so, there are pitfalls because adequate allowance is not made for adult mortality from natural causes. Some hypothetical figures will serve to illustrate this weakness. Suppose 100 adults have 80 fawns, and mortality reduces the fawns to 40 by the following year. "Productivity" would be figured at 40 per cent. However, should there have been an interim loss of 20 adults, "productivity" would be computed at 50 per cent (40 yearlings divided by 80 adults)—a seemingly incongruous value in the face of reduced herd numbers. A case in point is the North Kaibab herd, which declined from an estimated 36,627 animals in 1954 to 11,889 in 1955. Winter mortality was the primary cause for decline because legal hunting took only 8,058 deer. Yet "productivity" for the interval based upon the per cent of yearlings in 1955 to older deer was 26.6

per cent. Can there be any "net production" when natural mortality far exceeded, numerically, the number of yearlings added to the herd? This reviewer thinks not.

In summary, the reviewer wishes to emphasize that the few negative notes which have been raised do not detract from the bulletin's values. Major results, conclusions and recommendations are in no way affected. The publication contains much for anyone concerned with big game, be he technician, administrator or hunter.—W. LESLIE ROBINETTE, U.S. Fish and Wildlife Service, Federal Center, Denver, Colorado.

Poison on the Land. By J. Wentworth Day. Philosophical Library, Inc., New York. 1957. x+ 246pp. $6.00.

"If this book sows a few seeds of thought and action, it will have served its purpose." Thus the British author, J. Wentworth Day, summarizes his intentions in the introduction. This publication concerns wildlife and land management conditions in Great Britain.

The book is most timely, because of present concern over the influence on wildlife populations of chemical pesticides, fungicides, insecticides, and herbicides. *Poison on the Land* is a dramatic title, which together with the eye-catching dust cover ought to help sales. Such a volume should make the general public cognizant of some of the real and potential dangers in the widespread, unrestricted use of chemicals in farm and forest management. Unfortunately, in my estimation, Mr. Day's volume falls far short of this goal. The title is rather a misnomer, since only about one-fifth of the book has to do with chemical applications and their effects on wildlife. Part I, entitled "The Menace to Wild Life Today" contains most of the references to chemicals. In Chapter 1, Mr. Day warns the reader of dangers to the wildlife of the English countryside. His examples of what might possibly result from land misuse are a bit too broad, viz.: "The birdless fields of France, the gloomy forests of Germany and the vast timberlands of North America, where the only living sound is the cry of the 'whisky-jack' or the rustle of a porcupine, are ghastly reminders of what the reckless destruction of bird and animal life can mean" (p.3). The author mentions not only the use of chemicals as cause for the decline in game, but also changes in land ownership. Throughout the book Mr. Day is rather critical of public agencies, bureaucracies, and investigative committees. He begins his crusade with: "Forestry Commission plantations brood like clouds of doom on once-beautiful hillsides and wild heathlands" (p.4). It seems to me that criticism of this type might best be relegated to the editorial page of the local newspapers. Most of the second chapter, in fact nearly all of the information given on chemicals, is quoted from other sources. Some of the sources are cited, others are not. There is no bibliography. Quotations from a report by the Ministry of Agriculture in 1955, popularly called the "Zuckerman Report" (the entire title is never given), comprise most of the second chapter. Although Mr. Day cites this report for over ten pages, he alternately praises and condemns it with such comments as: "The working party came to the following conclusions which I think are worth giving in full" (p.23); "The committee's recommendations, pious and wordy as they are, do not really amount to much" (p.27); "There is a lot of common sense, platitudinous though it is, in these recommendations" (p.32); ". . . and they say, wisely . . ." (p.36); "The important points which emerge from this jungle of jargon . . ." (p.37). Chapters 4 and 5 have to do with myxomatosis and the rabbit. Many quotations are given that lucidly describe the rather unpleasant appearance of dead and dying rabbits. Mr. Day is against the introduction of myxomatosis, but for control of the rabbit by other means. In "The Fox at the Crossroads," he discusses just what, and who, constitutes fox hunting and fox hunters. Information is given as to the pound (£) value of the sport, along with the predatory or destructive potential of the fox. According to the author, hunting, and moderate control of foxes in areas where they are numerous, can be harmonious. "The arrogant man on a horse, and the loud-voiced woman, both of whom imagine that a red coat automatically transforms them into feudal autocrats, are the real enemies of hunting" (p.97). It seems that Mr. Day has touched upon a universal problem here. Part I contains two more chapters, one about the rat, the other regarding pollution in rivers. The case against the rat could have been adequately documented without the description of their feeding on human cadavers. The brief chapter on "Poison in Our Rivers" lists polluted rivers, with some impression of their former productiveness indicated by a listing of salmon catch data. Mr. Day recommends stricter laws and forceful administration.

Part II, entitled "The Value and Future of Game and Other Birds," contains Mr. Day's impressions, philosophies, and suggestions related to British game management. Perhaps the most concise way of summarizing the contents is to list the titles of the chapters. They are: "Bad Game Seasons"; "The Cash Value of Game"; "On Rearing and Keepering Pheasants"; "Forestry, the Pheasant and the Farmer"; "Winter Feeding of Partridges"; "The Mystical Woodcock"; "The Golden Bird" (red grouse); "Pigeons, the Feathered Plague"; and "Birds and the Farmer." In much of the material given to substantiate the relative economic good or harm done by certain species of birds, food-habits studies are quoted. The conclusion that "crop contents in any case give a representative sample of the food eaten" (p.138) is hardly warranted. The work of Middleton and Chitty on the food of partridges (*Perdix*) is adequately cited, but quoted without appropriate punctuation. Without the

original text, it is a bit difficult to tell just where the author resumes his commentary. In his discussion of partridge management, Mr. Day, although apparently familiar with much of the recent work by the Imperial Chemical Industries' Game Research Station, perpetuates the old fallacy that "inbreeding must be prevented as far as possible by breaking up the coveys or by introducing fresh stock from other districts or other counties" (p.131).

Mr. Day's experience in the purchasing and managing of shooting rights is evident throughout the second part of the book. In my estimation his commentary here gives a fair appraisal of game management as now practiced in Great Britain. Some of the techniques he mentions are, of course, as variable as the number of gamekeepers putting them into operation. The author has deftly placed a pound (£) value on many aspects of game management, wildlife, and shooting. It might be well for some American sportsmen to realize from this just how valuable their "free" hunting is in terms of dollars and cents. I like Mr. Day's moderate dealing with many species of predatory birds and mammals. Only too often when sporting men put pen to paper, they indulge in wholesale condemnation of all predatory species.

The title page includes a partial list of 28 books by Mr. Day. Although $6.00 for this volume seems a trifle high, it is distinctly readable and would be informative for those who wish to learn more about British game management.—TONY J. PETERLE, Rose Lake Wildlife Experiment Station, Michigan Department of Conservation, East Lansing, Michigan.

Wildlife Abstracts 1952–55/A Bibliography and Index of the Abstracts in Wildlife Review Numbers 67–83. Compiled by Lucille F. Stickel. U.S. Department of the Interior, Fish and Wildlife Service. xxii+321pp. (For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C.) $2.00.

The main parts of this useful volume consist of a 20-page list of abbreviations and publication sources, a 211-page classified list of 6,620 papers, publications and books, a 24-page author index, and an 86-page subject index. Similar in format to *Wildlife Abstracts 1935–51*, which contained about 50 per cent more entries, this new bibliography does not attempt to abstract papers. It does provide an efficient classification of the literature of wildlife management and conservation for the four-year period 1952–55, and it furnishes one with a very helpful index to 17 issues of *Wildlife Review*, which is so indispensable to our field.

The indexing, editorial work, and scholarship in this volume appear to be of a high order. Together with *Wildlife Review*, it forms an invaluable cornerstone to the foundation on which the technology of wildlife management rests today.—J. J. HICKEY, University of Wisconsin, Madison 6, Wisconsin.

The Law of Water Allocation in the Eastern United States. Edited by David Haber and Stephen W. Bergen. The Ronald Press Company, New York. 1958. xxxviii+643pp. $7.50.

This is a collection of 12 papers presented at a symposium sponsored by The Conservation Foundation during October 1956, together with an edited transcript of discussions by 39 invited participants. Six participants were associated with agriculture, 12 with law, and 14 with either Federal or state agencies. The conservation departments of Michigan and North Carolina were represented.

These essays analyze and evaluate a broad range of topics that include: (1) the riparian system in Massachusetts, North Carolina, and Michigan, (2) water-allocation experience in the 17 western states lying wholly or in part west of the ninety-eighth meridian, (3) water-law changes proposed in the remaining 31 states, (4) constitutional problems, (5) economic factors, including protection of business investments, to be considered in providing for utilization and control of the water resource, and (6) matters of administrative management.

Such a collection lacks somewhat in over-all coherence, but this drawback is partly compensated for by Professor Haber's introductory 13-page analysis of common law doctrines, of prior appropriation statutes, and of the position of those advancing major changes in water-allocation systems. Harold E. Thomas of the United States Geological Survey has also contributed an excellent résumé of principal problem areas in his article, "Hydrology vs. Water Allocation in the United States."

Conservationists studying these essays will observe that relatively little attention is given to their problems. Nevertheless, the book is worthwhile in focusing on those issues that conservationists must meet in dealing with present and future conflicts of interest between protection of fish, wildlife, and recreational purposes on the one hand and utilization of water for industry and agriculture on the other. A comprehensive concept of the underlying philosophies in each of the conflicting positions may be had by comparing these essays with those relating to "Recreation in the Age of Automation," which appeared in the September 1957 issue of *The Annals of the American Academy of Political and Social Science.* It will behoove game managers and other conservationists to have such an understanding as they plan for broadening the recreation program in this country.—RICHARD HARNSBERGER, College of Law, University of Nebraska, Lincoln, Nebraska.

OBITUARY

Earl C. O'Roke
1887–1958

With the death of Dr. Earl Cleveland O'Roke, Professor Emeritus of Forest Zoology, the University of Michigan and the wildlife management profession lost one of the foremost leaders in the study of wildlife diseases. Throughout his 28-year career at the University he was lovingly known as "the smiling Irishman." He died on January 30, 1958, of a stroke that was the second attack in a year and a half. Earl had retired in July 1957 with impaired vision, but he was planning to continue his activity in wildlife diseases and the study of travel in the western states.

Dr. O'Roke enjoyed a long and fruitful connection with the University of Michigan, joining the faculty as Assistant Professor of Forest Zoology in 1929. He had a wide and varied background, having lived on a farm in Kansas and having worked in South Dakota, Wyoming and California. The University of Kansas awarded him his B.A. degree in 1912 and his M.A. degree in 1916. He received his Ph.D. degree from the University of California in 1929. He served as collaborator with the Biological Survey and the Fish and Wildlife Service from 1932 to 1953 and was visiting investigator in diseases of wild animals at the University of California in 1950.

In addition to Professor O'Roke's tireless devotion to his students and his research, he found time during the war to assist in the preparation of a book *On Your Own*, which was used as a guide to servicemen in learning how to survive in the wilderness. Among his researches, three stand out as being of special significance. These are his studies of the diseases of quail, waterfowl and deer. He was best known for his original work on the transmission of *Leucocytozoon* disease by black flies to ducklings. He also initiated the first project attempting to trace the deer lungworm by the use of radioactive isotopes. Although the results were inconclusive, it was nevertheless a noteworthy first in a new field of great promise in wildlife-disease study. Probably Dr. O'Roke's greatest contribution to his profession was his training of graduate students. Many of his "boys" are now nationally recognized leaders in the field in which he pioneered.

In his private life, Earl was a warm friend to his colleagues and students and neighbors. He was especially well known for his rare sense of humor and his ability to compose verse that aptly expressed his amusement. He saw beauty in all of nature and especially loved the prairies and mountains of the West—his home country.

Throughout his lifetime he was a loyal worker with a wide group of scientific organizations, being a member of the American Association for the Advancement of Science, the American Society of Parasitologists, the Society of American Foresters, the Wilderness Society, and a charter member of The Wildlife Society.

Earl is survived by his wife, Cora Ann Morris O'Roke; a daughter, Mrs. Stuart A. Reading; and two grandchildren.—Warren W. Chase.

ERRATA

In my paper, "Field Key to Guard Hair of Middle Western Furbearers" in the Journal (22:95–97), under item 39, page 96, the word *top* should read *tip*.

—J. Howard Stains

In R. S. Dorney's article, "Ruffed Grouse Roosts as a Spring-census Technique" in the Journal (22:97–99), line 3, page 99, should read:

spring should be studied, to establish these dates

—Ed.

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